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NESTS AND NEST-BUILDING IN BIRDS: PART I

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TEN FIGURES

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1. INTRODUCTION

The nest and the bird are so closely associated that one promptly suggests the other. They fit like lock and key. Yet there are other nest-builders, both vertebrate and invertebrate, which fashion even more uniform, complex, and more remarkable structures than many birds; for among the social insects, the paper-making and mud-dauber wasps, the wax-secreting bees and wood-gnawing termites, not to speak of many true ants, build not alone to protect their young in infancy, but to house the entire colony, to store its food, and minister to the varied needs of all its members, young and old.

A few marine and many fluviatile fishes, certain *tree* toads which make *tree* nests, and among the nearer kin of birds, many lizards and alligators, not to speak of a great host of mammals, either build true nests, or rear houses, lodges, forms, or structures of some sort, in which to lay their eggs or young, or to conceal and guard both. It was left, however, for the modern birds to develop an ancient custom on a wider and somewhat different scale, for no other animals have ever possessed their tools in their present form,—breast, bill, feet, and wings—, and no

vertebrates below the level of man have ever carried the art of building to the same degree of perfection and elaboration of detail. It is further interesting to notice that the only invertebrates which feed their young, and care directly for their various needs, are bees, ants, and termites, and the only vertebrates, birds and mammals, all of which represent the greatest nest-builders of the world.

Both the eggs and the nests of birds, in relation to the builders, have often been the first objects to open the eyes and kindle the zeal of the born naturalist, and often too the only ones to arouse even a spark of enthusiasm for natural history in others, on whom the harder and dryer facts of science fall as on barren ground. The delicate and often beautifully colored eggs of birds, like the sea shells tossed upon the beach, have been sought by collectors for over two hundred years, but with all due regard for many students of exceptional merit, they seem to have led to little more than a pseudo science of oology, while we sometimes hear of the study of nests mentioned in undertone as "caliology." Biology does not scorn the shell of the egg, any more than the jeweller despises the case of the watch, but it points to the vastly greater interest and importance of the going mechanism inside.

It is a singular fact that with all the popular and scientific interest presented by the nests of wild birds, which have been celebrated as beautiful and adaptive structures from antiquity, and are found in every clime, this interest, with a few notable exceptions, should have stopped with an admiration for their beauty or a description of the finished work, with but scattering notes upon the variability of certain species in relation to habit and environment, and still less upon the actions of the builders at work. In many ways, it would be difficult indeed, from the standpoint of the student of instinct and behavior, to find a more unsatisfactory class of scientific literature than that which deals with the nests of birds.

Among a number of popular or semi-scientific books upon the nests and nest-life of birds, one of the earliest, by Rennie,[1] the editor of Montagu's Ornithological Dictionary, was excellent in its day, and like his other works on the "Habits," and the "Faculties of Birds," in spite of the errors which it must inevit-

[1] Rennie, James: Bird Architecture. London, 1831.

ably contain, it is still a useful compendium. The recent, more popular, or more restricted works on nests, like those of the Keartons,[2] and Dugmore,[3] are notable for their admirable pictures after photographs. Birds' nests are notoriously difficult to depict, and photography alone seems adequate to the task. Possibly the most elaborate representations of nests, not due to photographic art, appeared in a work of joint authorship on the nests and eggs of Ohio birds.[4] This Audubonian attempt at pictorial completeness consists of sixty-eight folio plates of eggs and nests in full size, colored by hand, and with descriptive letter-press.

Bendire's "Life Histories of North American Birds"[5] is our greatest treasury of facts pertaining to the nests, eggs, and breeding habits of American birds, but the observations recorded on the subject of nest-building are not very extensive. To the same class also belongs a considerable list of ornithological works from the days of Alexander Wilson and John James Audubon to the present time, in all of which the nests and nesting habits of birds have a prominent place, not to speak of the almost innumerable monographs and special papers in the principal languages, but since we are dealing with the subject from a somewhat different standpoint, it will not be possible to refer to many of these even by title.

I have given a brief discussion of nest-building in an earlier work, as illustrated in a limited number of common American birds.[6] Boulder Sharpe[7] has brought together in popular form much interesting matter pertaining to the nests of birds of the world, and a very sane discussion in brief of the subject of nidification within the avian class is given by Pycraft[8] in his excellent History of Birds, to which reference will be made later.

The papers on this subject which seem to have attracted the most attention are "The Philosophy of Birds' Nests," first pub-

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[2] Kearton, Richard and C.: British Birds' Nests. London, 1895; revised ed., 1907; also Our Rarer British Breeding Birds. London, 1899.

[3] Dugmore, A. R.: Bird-Homes. New York, 1900.

[4] Jones, G. E. and Shulze, E. J. (with later co-operation of Mrs. N. E. Jones and Howard Jones): Illustrations of the Nests and Eggs of the Birds of Ohio. Pls. i–xlviii, pp. i–xxxviii, xxxviii a–d, 41–329. Circleville, O., 1879–86.

[5] Smithsonian Contributions to Knowledge, vols. xxviii and xxxii. Washington, 1892 and 1895.

[6] The Home Life of Wild Birds. New York, 1905. Chap. XI.

[7] Wonders of the Bird World. London, 1908.

[8] Pycraft, W. P.: A History of Birds. London, 1910. Chap. XI.

lished in 1867, and "A Theory of Birds' Nests," which appeared in the following year, by Alfred Russell Wallace; both have since been printed in revised form, and presumably still appeal to a diminishing number of writers. These interesting essays have received ample criticism of various sorts, and although it is not likely that students of animal behavior at the present time could accept much of the philosophy which they offer, this should not alter the high and just esteem in which their venerable author is universally held. Wallace was tempted to leave the solid ground of instinct for the pitfalls of analogy, and to fill the gaps in observed facts by unwarranted inference: Man builds by memory and imitation; why not also the birds? He contended that in nest-building instinct had been assumed not alone for birds but for the social insects as well, and that for the former it could be proved only by showing that the young of a wild bird, when artificially reared would inevitably reproduce its own specific type of nest, without tuition of any sort. In his opinion the few cases in which this crucial test had then been applied failed to support the prevailing theory of instinct. While we do not consider that the few experiments which have since been recorded uphold any other theory than that of instinct, it is to be noted that the long confinement under artificial conditions, commonly required in such tests, is almost certain to disturb, if not to profoundly modify the reproductive activities.

Wallace's odd notion that the nestling was more eager to learn than the "whining schoolboy creeping like snail" to the "nest" of knowledge, is thus naively expressed: "But surely the young birds *before* they left the nest had ample opportunities of observing its *form*, its *size*, its *position*, the *materials* of which it was constructed, and the manner in which these materials were arranged. Memory would retain these observations until the following spring, when the materials would come in their way during their daily search for food, and it seems highly probable that the older birds would begin building first, and that those born the preceding summer would follow their example, learning from them how the foundations are laid and the materials put together." His earlier idea that young birds made mental notes of the nest in which they were reared in order to be able to reproduce one on the same model later in

life,—not to speak of the assumption that such nestlings have concepts of artificial, as distinguished from natural objects, or that they have abstract ideas at all,—is no more fanciful than that birds build on the copy-book plan, or under the tutelege of older and more experienced mates.[9]

The story of the mud dauber wasp which builds a unique tube of clay for its eggs, and stores it with food for young which it never sees, or of the spider's web and egg-cocoon, so faithful to " copy " which is never used, of the caterpillar which weaves a chrysalis case but once in its life yet does it to perfection, not to speak of similar illustrations by the hundred,—is not needed to refute any theory of nest building based upon imitation, memory, or intelligence of whatever degree. The proof of instinct in the nest-building activities of birds lies in the stereotyped behavior of the builders at work, as well as in the stereotyped character of the nests of the different species, when these are viewed in a proper light; it is seen also in the relation of nest-building to other phases of the reproductive cycle, as well as in the correlated activities of adult and young. No one for a moment could attribute mental powers below the lowest plane of association to the nestlings of passerine birds representative of the highest existing order, who had watched their behavior or tested their capacities. On the score of behavior alone the evidence is now conclusive that birds do not build their nests from imitation or experience: they require no visible standard, plan, or copy; they need no experienced mate or tutor, but like Santa Claus, they "go straight to work," and finish their task, without hesitation and commonly alone, whether it be in the gloom of a cavern or chimney, the glare of the tropical sun, or the bustle of a city street. Instinct alone furnishes the building impulse, and in spite of many fluctuations, whether due to experience, disturbance, or to any influence of the environment whatsoever, it holds the builders wonderfully true to their ancestral types.

In the second paper referred to, Mr. Wallace endeavored to show that the nesting habits of birds were largely responsible

[9] Craig has shown that inexperience in pigeons is no bar to successful mating, nest-building, and care of the young, only, as he says " their efforts lack something of the precision and the promptness which signally characterize the work of experienced birds." Craig, Wallace: The voices of pigeons regarded as a means of social control. *American Journal of Sociology*, vol. xiv, 1908.

for the gay and attractive colors which so many of them display to man's great delight, if not to their own. He divided birds into two groups, based solely upon whether the eggs, young, and sitting parent,—that is the contents of the nest,—were exposed or hidden from view. In the first division we should find those species which canopy their nests or frequent dark or cavernous places of any kind, while the second would embrace all which sit in the open, like a nighthawk, or which build nests open from above, as in by far the greater number of modern birds. Assuming that nesting habit was strictly correlated with structure, and was more stable than color, he inferred that all such species as the parrots, toucans, and kingfishers, which are known to be equally brilliant in both sexes, the intensity and equality of color was due to the habit of concealing their nests or eggs.

By nesting in hidden places both sexes of all such birds were placed on an equality, so far as protection during reproduction was concerned, so that sexual selection and other causes of specific change were allowed to act unchecked, whether in the production of bright colors or conspicuous markings. Female birds, on the other hand, which had brilliant mates and built open nests, were almost always obscure in the coloring of their upper or exposed parts. The fact that both classes of nests occur in such birds as the flycatchers, which are dull in either sex, was dismissed by Mr. Wallace with the remark that such coloring merely served to protect the parents at other times than when engaged in reproduction, the structure of the nest being dependent upon the needs of the offspring.

Mr. Wallace was certainly right in assuming that coverings of the nest in the form of canopies or shields serve more or less effectively to protect its contents, but in error in limiting the needed protection, as he seems to do, to concealment effected in these ways. Protection indeed, in some measure, there must be, but aside from every other question involved, it can be shown that sharpened instincts are frequently a greater asset in securing this protection than anything connected with the nest itself.

Without entering the labyrinths of the color question, we shall endeavor to show in the following section how protection is actually secured during the nesting period by certain species, regardless of color in the adult or of the open or closed nature

of the nest. Whatever conditions may have prevailed in the past, it is easy to see that the facts of color and nesting habit are too diverse and too complex for any such simple analysis. Few species have yet been studied with sufficient care with reference to all the factors involved, and no theory can have any weight which does not consider all the elements of the problem, and in particular the instincts of the adult in relation to those of the young.

A work on nests by Dixon [10] contains much interesting matter on the structure of nests as well as upon the nesting habits, but little on the behavior of the builders. The author was a correspondent of Mr. Wallace, supplied him with some of his facts, and echoes his theories. His attitude on the problems of instinct and intelligence in birds is apparent in his preface: If a "bird's nest" were really "a most graphic mirror of a bird's mind," as this writer asserts, it should have given us long ago a true picture of the mental qualities of the builder. This it has failed to do, and as I have shown in another place, the nest in relation to the builder, has been the subject of misinterpretation at more than one point.[11] To the writer referred to, "it is the most palpable example of those reasoning, thinking qualities with which these creatures are unquestionably most highly endowed," and yet we are presently told that "our lack of information relating to the manner in which the nest is made in the majority of species is almost complete." The reader is thus left to wonder how a bird's nest can be the "graphic mirror" of great mental powers, if we do not know how it is built. The nest, this writer continues, is primarily a utilitarian structure, and he concludes that it must be a work of great intelligence, because it is so wonderfully adaptive, even though it is generally admitted that "order is heaven's first law," and fitness one of the most striking characteristics of living things, extending even to the parts, properties and behavior of the smallest microscopical cell. To quote further, "A young bird three or four days old is capable of considerable powers of memory and observation, and during the time that elapses in which it is in the nest it has ample opportunity of gaining an

[10] Dixon, Charles: Birds' Nests. London, 1905.

[11] See The Home Life of Wild Birds, chap. xi, and The Instinct and Intelligence in Birds. *The Popular Science Monthly*, vol. lxxvii, July, 1910.

insight into the architecture peculiar to its species. It sees the position of its nest, it notes the materials, and when it requires one for itself, is it so extraordinary that, profiting by such experience, it builds one on the same plan?" To the question thus temptingly put, we should be inclined to answer: No indeed! Not if the nestling is such a precocious prodigy as you suppose, but we could as soon believe that it might evolve a kind of Gothic architecture, by seeing the trees meet over its head, as our early ancestors are supposed to have done in the woods of Germany. One might be inclined to further ask what kind of mental notes the young of the esculent swiftlet (*Collocalia fuciphaga*) would be likely to make, inasmuch as they are born in a darkened cave, and on a little bracket of glue, which represents the hardened secretion of the salivary glands of their parents,—or the precocious chicks of the ocellated Megapode, which after hatching have to dig their way to liberty through several feet of earth, and in order to determine the remarkable character of their peculiar mound nests, man finds it necessary to prepare, as it were, a geological section of the ground. Moreover, the Megapodes which have bred in the Zoological Gardens of London, have made their mounds and set their eggs within it, large ends uppermost, true to the traditions of their race.

The word "nidification," which signifies the act of building the nest, owing to the lack of knowledge, has become perverted to mean the structure of the nest, so we are not surprised to find in the article under this head, in Newton's most excellent Dictionary of Birds, but few lines devoted to the subject in the strict sense: in these few, moreover, we are told that "the tailor-bird deliberately spins a thread, and therewith sews together the edges of a pair of leaves to make a receptacle for its nest; while the fantail warbler, by a similar process of stitching—even making a knot at the end of the thread—unites as a sheltering canopy above its nest the upper ends of the grass stems amid which it is built." One might be inclined to ask: Does this warbler really knot its threads, for if it does so, the act must be regarded as truly wonderful? More cautious authors fail to mention it. Men and women certainly spin threads, drawing and twisting them by hand or machinery, and knot them for various purposes, and they do these things deliberately,

with a definite end in view; spiders also by courtesy are said to spin, but I do not think it can be proved that birds deliberately either spin threads or tie knots. I have a nest of the oriole, which is a felt-work of fibers, shot in and out, through and through, looped in almost every conceivable way, thousands of them, and in a sense no doubt knotted at many points; further I watched the building of this nest, and I know that the work was done with a speed that taxed every resource to follow it, and that such looping or "knotting" as exists, far from being deliberate, was the inevitable consequence of a stereotyped method of work, comparable to the turning and molding movements of a building robin, or gull. It is not necessary to emphasize further the need of ample corroboration of such remarkable statements as we have quoted, for much of the difficulty in dealing with the literature of nest-building lies in the very lack of such requirements.

Although my own studies in the field have been limited to a few common American birds, they are offered at the present time in the hope of directing the attention of other students to a most interesting but singularly neglected field. Not only do we need careful observations on the many representatives of the seventeen thousand or more builders of nests throughout the avian world, but we need repeated studies on the work of different builders of the same species as well as upon successive operations of the same individuals in the same or successive seasons. Data of this sort to be most satisfactory, should represent the whole phase of behavior or building activity from the start to the finish of a given nest. In many cases, to be sure, from one cause or another such observations are either extremely difficult or impossible, but in other and equally important cases they are easy, the time element only standing in the way of an observer, who, like myself, is liable to be called away by other duties before his task is finished. In the case of an oriole for instance, it would mean to be on the ground, at a point where the birds could be clearly seen and their movements followed for the best part of three or even four days, or from the time the site is chosen and the first threads are laid to the putting of the last stitch in the "hammock." The importance of following the activities of more than one set of builders is seen from the records of the robins which will be given later. I have merely

scratched the surface at a few points only, but suspect that what has been uncovered will prove to be quite characteristic.

2. THE NEST AND THE PROBLEM OF PROTECTION

When nest-building is studied in relation to other correlated instincts of the reproductive cycle, as well as to the behavior of the mated pair, many dark places begin to lighten, and many enigmas vanish.

As we have tried to show in earlier papers [12] nest-building in birds is to be regarded primarily as one of the serial instincts of the reproductive cycle, the successive terms of which rise and wane in due order when properly and normally attuned in the builders concerned. Not only are the general instincts serial and harmonized, as seen in migration, mating, nest-building, egg-laying, care of the young in the nest, and the like, but some of these arbitrary terms, like the last, are very complex. There is not only an annual cycle, but what may be called a daily "cycle," in a different sense, made up of recurrent acts varying in accordance with the degree of progress attained or the degree of intelligence exercised, whether it be building the nest, brooding, or feeding the young. In building, the acts are serial, and often in a high degree stereotyped, while in what may be also called the feeding "cycle," the round of activities, though more complex, follow in similar chain form. The search, capture, and treatment of prey, return to the nest, testing the throats of the nestlings, and waiting for the swallowing reflex in each, inspecting, and cleaning young and nest, all go on seemingly with clock like regularity, day after day, subject to slight changes as noted above, and to the influence of mate over mate on the one hand, and of parent over child or child over parent, on the other.

The nest must anticipate the egg, and not the egg the nest, but the order and harmony which commonly prevail are subject to many disturbing influences, leading now to a premature laying of the eggs, to a scamping of the nest or omission of nest building, to the sudden breaking of a first cycle, followed by the

[12] See especially Analysis of the Cyclical Instincts of Birds, *Science*, N. S., vol. xxv, nos. 645–646, 1907; also Instinct and Intelligence in Birds, *Popular Science Monthly*, vol. 76, pp. 532–536, and vol. 77, pp. 82–97, 122–141, 1910; Life and Behavior of the Cuckoo, *The Journal of Experimental Zoology*, vol. ix, pp. 169–234, pls. 1–7, 1910.

beginning of a second, to the desertion of backward young in favor of those which have left the nest, or of the entire brood when the maternal impulses are swamped by the rising migratory instinct, by a recrudescence at the close of the season, of a cycle which is never finished, as well as to a great variety of eccentric behavior. Whenever a " stitch is dropped," as when the annual cycle is broken by fear or accident, they must usually go back in order to pick up the thread; in other words, a new cycle is begun, and commonly by building a new nest on a new site. Whenever the old nest is chosen as a site for the new, and this may repeatedly happen, we have in some cases a remarkable production indeed,—a storied or compound nest. Whenever fear is simply repressed by the brooding impulse, or through other conditions, a loss of eggs is very often repeatedly made good by the production of more, checked only at last it would seem by the capacity of the ovary, and the physical resources of the individual. Some species normally repeat the breeding cycle more than once during the season.

In all the higher animals the store of nervous energy is expended mainly for three prime purposes, for getting food, defence from enemies, and in reproducing their kind. It is during the breeding period of birds in particular, that emotion is keyed to the highest point, when every power is likely to be taxed to the uttermost, and the cup of nervous energy drained even to the dregs. Individual struggle is then complicated by the presence of offspring, which may call into play at one time or another every sharpened power, strategy, or device, with which nature has equipped them to fight their hardest battles, for a strong and useful weapon,—fear and retreat,—is often for a time so dulled that self-sacrifice, however needless, is frequently demanded.

The more brilliant coloring, the joyous or ecstatic song, the keener instincts as seen in the greater caution, alertness, or pugnacity, displayed at one time or another in this cycle of events, and after a period of recuperation, all bear witness to the intensity of emotion, which in all the higher exponents of their class, characterize the climax of reproduction. It is a sane and safe conclusion that no mental powers with which this race is endowed are ever wholly withdrawn from the most critical period of their lives. This is why the round of daily life at other times

seems tame and humdrum compared with the guarding, fighting, luring, and kindred outbursts of energy, which so commonly attend the breeding cycle of birds.

It seems to be the aim of the bird, when possessed of the breeding impulses, to find a hole in which to deposit its eggs, or barring this, to make one for itself, " building around a hole," as it were, as Pycraft says of the quaker parrot. But in many cases this protective pocket becomes a graceful, symmetrical " cup," or " saucer," as true as if thrown on a potter's wheel, or a nicely modelled " purse," " hammock," or " stocking," suspended to adequate supports, or a neatly molded and arched " oven," or even an excavated chamber, with entrance tube or tunnel, when underground, often running five or ten feet clear from the surface.

Speaking in general, it is undeniably true that the bird's nest is built primarily for protection, which is directed either to the eggs, to the eggs and young, or to the eggs, young, and adult combined. But the ultimate or adequate protection secured is not dependent upon the structure of the nest alone, which so far as the adult and young are concerned, is often a trap and a snare which leads to their destruction.

We will now consider some of the more obvious ways in which the nest ministers to this prime need, leaving a fuller discussion of certain factors for a later section. It is useless to generalize when it is so obvious that the elements of the protection secured vary with the species, it being now the nest-structure, now its position, or again keen instincts or other bodily powers which tip the scale of protection to the side of safety for the adult, its progeny or both.

To cite a few cases in illustration of this phase of the question of protection: in the tropical hornbills (*Bucerotidae*) the nest is the strong factor in ensuring the safety of all concerned, for the sitting female is barricaded against attacks from outside enemies in a wholly exceptional manner, though suggesting indeed a habit of the European nuthatch, of partly closing its nest-hole with mud, or the American red-bellied nuthatch in smearing its entrance with pitch; in the hornbill the doorway is both smeared and plastered up with mud and a glutinous secretion until it is reduced to a small opening, but just large enough to admit the food, which is passed in by the males, and to improve the chances

of defence if the prisoner is attacked. At another extreme we find the tree swifts (*Macrodipteryx*), of India and Japan, making the smallest nests, in proportion to the size of the builder, known. In one species indeed (*M. comatus*), it is just large enough to frame and hold the single large egg, but thin as "parchment," and so frail as to be unequal to bear the weight of the builder; accordingly this bird, when incubating, sits over rather than on her nest, resting her feet on the twig to which her diminutive "egg-cup" is attached. Such a nest can afford little protection to the young, and none whatever to the adult.

A good instance of protection secured mainly through the fighting and guarding instincts of the adult is afforded by the American kingbird; though dull black above and white below these flycatchers are much in evidence about their nests on account of their bold aggressive natures. They build not only open but highly conspicuous nests, often placing them on a dead branch, ten or fifteen feet from the ground, and they lay white, boldly spotted eggs. Few of our birds develop the guarding and fighting instinct to a higher degree, the male in particular, which never hesitates to assail any marauder which enters his premises. From his swift attack and fiery temper both hawk and crow are quick to beat a retreat. The kingbird seems to advertise its open nest, and because of its pugnacity, it can perhaps afford to do so.

In many of the eastern species of *Icterus* both sexes are equally brilliant, but in our Baltimore oriole the female is more quiet in dress than her firebrand of a mate. It is improbable that this oriole would be any less protected when brooding eggs or young if she donned a gayer dress, or that she would be any safer at this time were the nest canopied, or completely concealed from view both from above and below, for in this instance the great element of protection lies in the position of the nest, in relation to all the instincts of the adult, and in spite of certain actions of the young. Their common method of stringing their nests to small, pendent, swaying twigs, and often at a considerable height, renders them practically immune from most attacks of cat, squirrel, snake, jay, or crow. That it is the inaccessible position of the elastic purse-shaped nest that protects the young oriole is shown by a trait which develops a little later. When about twelve days old these young begin to call loudly, at fre-

quent intervals through the day, and with a sort of rolling cadence, the degree of emphasis evinced corresponding to their hunger and excitement at the moment. This cry is thoroughly characteristic, and serves to advertise the nest to the countryside, and to every enemy capable of associating the cries of young birds with good living. On one occasion, in the course of three hours walking I found six nests of this oriole by the aid of the calling young alone; so upon the basis of any theory like that propounded by Wallace, we should have to ask, why should nature at one moment be so careful of the mother in order that she may shield and cherish her young, and at the next suddenly betray these young to their enemies?

To avoid tedious repetition, we shall at once try to analyze this protection which all birds receive in varying measure, when reproducing their kind and through the main channels or factors as given in table 1, namely, through specialized instincts (i), through their volition or intelligence (ii), and lastly through bodily structure (iii), as in external form, color, weapons, and the like, in more or less direct relation to every power possessed. Our attention for the present, however, is directed mainly to the instincts. The known facts could be expressed in other ways, and drawn out to far greater length, but this rough analysis will answer if it serves to illustrate the complexity of the problem of protection and the cardinal rôle played by instinct. In all such activities instinct comes first, and whatever its ultimate bounds may prove to be, intelligence is certainly subordinate.

It seems to be obvious that protection through concealment of the nest may be rendered equally effective in many ways, as well by dense foliage, as by remote or inhospitable surroundings, as well by adapting a natural cavity as by drilling an artificial one, by a temporary covering of leaves, as by a constructed permanent shield, which serves to modify the weather, if it sometimes fails to bar the monkey, the squirrel or the snake. It is equally clear that special instincts, whether of pugnacity or of any artifice which successfully foils an enemy, may be of far greater service to the offspring than any thing peculiar to the nest itself. To illustrate protection of this character, we will let the behavior of a common American bird suffice,—the bobolink, and if any one still believes that the structure of the nest is the prime factor in securing the protection of its con-

TABLE I

Analysis of the means through which Protection is secured by Birds during the Period of Young

PROTECTION (of eggs, young, or adult) in reproductive cycle.	(I). Through Instincts.	(1). Concealment or means to effect escape, other than noted below.	(a). Through special instincts, or artifices in adult or young.	Feigning, and luring; call notes and danger signals; behavior in fear, and attitudes of various sorts; transference of eggs or young, and raising or changing position of nest; bringing damp seaweed to nest, or wetting eggs after bathing (?), in osprey and other species; soiling eggs with excreta in eider duck, and all similar beneficial acts of reflex type.
			(b). Covers of the nest or its contents.	Natural, as when placed in caves, holes, or cavities of any description. Dense foliage or natural obstructions.
				Artificial (through parental effort), as in coverings of sand, feathers or vegetable products, constructed canopies or shields, as well as in "fresco" on outer wall of nest.
		(2). Care of eggs or young, in or out of nest, including brooding, feeding, shielding and cleaning young, or exceptionally providing them with water.		
		(3). Guarding and fighting, in relation to fear; instinctive imitation, and all forms of social influence and relations, when beneficial.		
	(II). Through Intelligence; modification of instincts through experience.			
	(III). Through Structure.	(1). External form of egg, (young), or adult, with or without the aid of color.		
		(2). Structure of adult or young, in correlation with instincts and every bodily power.		

tents, let him try to find the open, grass-lined "cup" of this bird, imbedded in the ground of any field or meadow, which it frequents. I think that many life-long students of birds would have to confess that they had never outwitted the strategy of this admirable, though sometimes destructive species.

Merely to be sheltered from the weather is at times as important as to be hid from enemies, for the tender nestlings of many passerine birds are certain to suffer if exposed to the full blaze of the sun, and it is probable that many die in consequence, even though brooded and fed. Very often no doubt the nest favors and regulates the access of heat and moisture, and in the presence of non-conductive materials often tends to effect an equable distribution of both, while preventing their undue loss. The importance of such secondary uses of the nest, however, are likely to be exaggerated, and an exhaustive array of examples might show that the "fits" and "misfits" were about equal. Such birds as ravens, crossbills, or eider ducks, which nest early or in high latitudes, where the snow lingers, and would seem to require a warm nest in consequence, are indeed credited with lining their cradles with wool, feathers, or in the case of the eider with down plucked by the female from her own breast. Yet this simple adjustment is not always made, for the great horned owl, which also breeds early and at times in the coldest and most exposed situations, is often content with the rudest sort of a nest. The emperor penguin, indeed, which incubates its large single egg through six of the coldest weeks of the Antarctic night, with the temperature ranging far below the freezing point, sometimes dispenses with a nest of any description; yet nature has aided this bird in a most unique way, by giving it a warm coverlid of down, a feathered fold from the under side of the body which hangs like a curtain over egg or young, and during incubation the egg thus screened rests on the feet of the sitter; there is no pouch, and the egg is not carried about as was once thought, but it is shifted from one parent to the other, both taking part in the long wearisome vigil.

We have seen that the nest, though essentially a cradle for the eggs or young, may become in certain cases a sort of temporary home, and afford a measure of protection, if not comfort to the family. Yet it is commonly abandoned abruptly and

forever by both old and young the moment the latter become independent, that is when its purpose has been served; the main exceptions to this common procedure are to be noted only in such species or individuals which use the site of the old nest for that of a new, either in the same or successive seasons. In a few cases the young repeatedly leave the nest and return to it again for a brief season, as in some of the swallows and swifts, but this seems altogether exceptional. The rather strong association which the young of most altricious birds form with their nest in the course of their brief stay within it is quickly broken by the still stronger influences which draw them away, whether it be fear, hunger, or parental influence, for it is the young, always the *young*, in which the commanding instincts of the adult are centered, and about which their lives revolve,—but only until these instincts are satisfied.

Protection through guarding or concealment is the essence of nest-building, and we may be sure that all modern birds both concealed and guarded their eggs, if they did not at one time build proper nests. Certain it is that some of them like the European cuckoo, falter or fail in this work at the present time through the loss of an instinct which their ancestors displayed. All possess the same tools, however much they may vary in form, size, or strength, and failure to build nests at the present day cannot be attributed to clumsy tools or to any structural peculiarity, but simply to the lack of inclination or impulse; in other words they have failed to develop the building instinct; protection in all such cases has been acquired in other ways. Says Wallace: "The clumsy hooked bills, short necks and feet and heavy bodies of parrots, render them quite incapable of building a nest," but behold the quaker parrot "turning the trick," and as Pycraft points out, building a great domed nest of sticks, with entrance at side.

The actual nest structure is certainly in the long run well adapted to the needs of the offspring, the parent, or to both; it is a refinement merely of simpler and more primitive means of obtaining protection. The character of both egg and nest represent but one or two of many variables, and while often important, one or both may become negligible quantities in securing the protection needed. Thus, primitive birds undoubtedly made or adapted natural holes, and laid white eggs like nearly

all reptiles at the present time, and many have made a success though sticking to the rut of ages; in many too such as parrots, woodpeckers, and pigeons, the eggs have grown whiter, if anything, despite all change which may have ensued in the family or species; some too like the magpies have changed their nesting habit long after they acquired richly pigmented eggs. All questions of comfort to sitter or young, or even protection from the elements, with the exceptions noted, in dealing with the class, must be considered as of secondary importance to concealment

FIGURE 1—Open nest with pure white eggs of mourning dove, *Zenaidura macroura*, removed from support; shallow saucer or platform of loose twigs and rootlets. Simple form of statant type.

and to protection by other means; we know that they are often discounted, at whatever cost.

To recapitulate: any theory of nests which lays the main emphasis upon the color of the adult or young, or upon these factors in relation to nesting habit, must be unsatisfactory because it cannot be generally applied. Any theory of organic evolution must account for all the characters of such animals or for none. The theory of selection gives as good an account of the nests of birds as it gives of their structure, colors, or instincts, but no better. In dealing with the nests there are

many variables to be reckoned with, and each species must be considered separately in reference to them all. If the most important variables are color in adult, egg, and young (*c*, *c i*, *c*2), the correlative instincts and powers of adult and young (*c. i.*), and the nesting habits (*n. h.*), their relative scale of importance in a given species with reference to protection at a given period, may stand as *c*, *c.i*, *n.h*, while in another species this order may be reversed to *n.h*, *c.i*, *c*, or with the main stress laid upon instincts, to the apparent neglect of any of the phases

FIGURE 2—Nest and egg of rose-breasted grosbeak, *Habia ludoviciana*, removed from support; fairly deep, symmetrical cup; loosely molded of twigs only, the finest added last; statant type of increment nest.

of color or even of the structure of the nest. To hazard a pure conjecture, the apparent contradictory nature of color phenomena in such animals may be due to the fact that their position in the scale of selected values has shifted, perhaps more than once, and been overlaid in consequence of the greater importance of other factors; the more elusive perhaps, but none the less important are the correlated instincts of adult and young.

"*Perfection*" *in Nest-Building*. The nests of birds are often described as more or less perfect or imperfect, according as they seem to measure up to the standard of the species. Imper-

fect or poorly constructed nests have been often attributed to the youth or inexperience of the builder, but in most cases, as it seems, upon insufficient grounds. The theory of instinct requires adequateness only in the first nest of any builder, never absolute conformity; we should expect the first nest of a robin to be as adequate for the purposes to which it is put, as the first nest of a mud dauber, or the first egg-cocoon of a spider, but we should not expect so great conformity to specific type in the more plastic bird, where practice must tend to make "perfect," and where the impulses which are due to heredity are modified in a far higher degree by experience. While observations under this head are almost nil, suspicions abound, and we would suggest that the question of imperative need for a nest, due to disturbance of any sort, whether from enemies, the weather, or a lack of the mutual attunement of the serial instincts themselves, cannot be left out of the account, although it must be admitted that they are often difficult to determine.

Aside from conformity to specific type, the best single criterion of perfection in nest-building is fitness or adaptability in the species or the individual. Yet many cases could be cited in which nests conform admirably to specific type, but are rather poorly adapted to protect either eggs or young, even in the situations usually chosen. Thus the neatly molded grass and hair nests of chipping sparrows are commonly too thin and flimsy, and too insecurely anchored to their supports to stand the tests of wind and weather to which they are apt to be subjected; the abundance of such birds seems to be due more to fertility and persistence than to skill in building. There are other birds, again, like some of the terns, which have never learned that a bare, wind-swept rock is a poor cradle for even a pyriform egg, though they have doubtless tried the experiment for ages, or that a rock-pocket is liable to fill with rain water and drown their progeny, whether egg or young.

There are birds in which a definite type of nest does not seem to have been established, yet it must be admitted that the significance of variation in such cases has seldom been determined. Thus, certain Indian wren-warblers (*Prinia*) sometimes suspend their nests by stitching together a few leaves, like the tailor-bird, or dispensing with such support, model a simple cup like so many other species. Such birds seem to be the despair of

collectors, for Mr. H. O. Hume, at one time editor of "Stray Feathers," thus speaks of their work: "Birds like these, which build half-a-dozen kinds of nests, ought to be abolished! They lead to all kinds of mistakes and difference of opinion, and are more trouble than they are worth." [13]

The arctic tern at Matinicus Rock, Maine, seems to follow no rules, but a plausible interpretation of such behavior can be given. With Baltimore orioles on the other hand great uniformity prevails: their cradles never fill with water and drown their

FIGURE 3—Pseudo-suspended nest of magnolia warbler, *Dendroica maculosa*; rim fixed to forking fir twigs, and here shown suspended to them; underlying branch on which cup was molded (see fig. 5), cut away; walls thin and loose; statant type of increment nest.

progeny, and though "endlessly rocking," they are seldom torn by tempests or reached by enemies. The antithesis of all these conditions is presented by the terns, which are preëminently social and breed in communities. The variations which they present seem to be due to the inhibitory influence of the social bond. The breeding cycle of this tern is clearly disturbed at every point by the influence of the tern *Bund* or society. If this is the case then variations in nest building would be proportionate to disturbance suffered, and might possibly be greater

[13] Sharpe, Boulder: Op. cit., p. 220.

on a small island inhabited by man (for Matinicus possesses a lighthouse), than in more secluded places. (See section 5.)

In considering the " perfection " of the nest we cannot overlook the fact that the mutual attunement, or synchronization of the instincts of any mated pair may in any case count for much. Thus, Craig,[14] who has emphasized the importance of this condition, has shown that in pigeons, the serial reflexes of the reproductive period, to produce the best results, not only must be attuned in the individual, but must be synchronized in the pair; male and female act as a unit, by a process of mutual adjustment or social control, now with impelling, and now with inhibitory effect, based on suggestion; whenever this mutual stimulus and response are ineffective, or when the male and female " chronometers " are dissynchronous, the pair are ill mated, and the results of the union are deficient or abortive.

We shall see in a later section that as a rule both sexes play a complementary part in nest-building, and that while the rôle of the female is mainly constructive, that of the male is more variable, but with a few possible exceptions at present known, equally necessary. In the American robin, to use a familiar instance which is probably repeated in hundreds of its order, the male builds but sporadically, his chief part being that of guardian and incentor to action. Thus, in such a case, the character of any given nest would seem to be determined not only by the specific type molded by heredity, by all the influences of the environment including that of the weather, and the factor of experience, embracing whatever adaptive intelligence may be available, but by the mutual reactions of the builders themselves. The male robin, though he bring not a stick or a straw to the nest site, by his pugnacity, his stimulating ardor or lack of it, may effect or even control certain characters of the nest.

3. THE CLASSIFICATION OF BIRDS' NESTS

We now propose to examine the nests of birds in order to ascertain what is essential to general and specific types of structure, and what significance variations from such types possess. Upon this subject no little misunderstanding has arisen; but this is in a measure inevitable, since the nests of wild birds are commonly examined and described as finished structures, with

[14] Craig, Wallace: Op. cit., p. 95.

little or no knowledge of the conditions under which they were produced, or of the variable factors indicated in the preceding section.

Aside from what may be regarded for the present as sporadic or wholly exceptional cases, I think it can be shown that specific variation of biological importance in nest-building is less than has been supposed, and that much indiscriminate speculation has arisen from confusing the non-essential with the more stable and important characters. Nevertheless I recognize the difficulties of the subject, and the present discussion is offered by way of suggestion for future observations, in what seem to me the right directions. Certainly the highly uniform and stereotyped characters of the nests of birds, in relation to the uniform and recurrent behavior of the builders, of which they are the visible expression, is the most impressive lesson which they teach, as it is the unimpeachable witness of the ruling hand of instinct in all nest-building operations.

Although there is no typical bird's nest in a strict sense, there are specific types of nests, as well as general types, based on typical activities of the builders. We shall consider the general types first. A classification of the nest of birds upon the basis of behavior is given in table 2, but that it is purely tentative need hardly be emphasized. No classification in sharply defined lines, is probably either possible or to be expected; moreover no classification can approach finality, until far more is known than at present upon the whole subject of nidification, and especially upon the behavior of the mated birds, and the significance of variations in their products.

The Caprimulgidae, of which the American nighthawk and whippoorwill are typical, represent a considerable number of birds which at the present day neither build nests of any sort, nor adopt or adapt cavities of any description to conceal their eggs. Yet it is interesting to notice that some of them become as attached to their chosen brooding places, as martins or woodpeckers to their adopted trees, and nighthawks,—presumably the same individuals,—have been known to occupy the same rock of even the same patch of ground for many successive seasons.

We regard the sand pile or mound of earth and leaves heaped over its eggs by Maleo or true Megapode (*No. 1* of table 2) as

TABLE II

Classification of the Nests of Birds on the Basis of Behavior

NESTS OF BIRDS.

- (1). *Primitive Nests*, but not necessarily of most primitive type: for concealment and incubation.
  - Earth and mound nests of Megapodes (Maleos and brush turkeys), in which the eggs are either buried in the ground like a turtle's, or in a great heap of leaves and rubbish, which serves as an incubator.
- (2). *Secondarily Adaptive Nests*, probably in some cases of primitive form: for concealment and protection in other ways.
  - Pertaining to all birds which use natural or artificial cavities of some sort, with little or no change (but never completely of their own making), or the disused nests of birds or other animals.
    - (a).[1] With no change: many owls, and parrots.
    - (b).[1] Partly constructive: bluebirds, many titmice, hornbills, European nuthatch.
- (3). *Primarily Adaptive Nests* (with reference to builder) mainly. Usually associated with greatest efforts for concealment and other means of protection.
  - i Individual (independent) nests.
    - (a). Excavated (mainly).
      - (1). In earth, with little or no materials added from without: kingfishers, sand martins, petrels, puffins.
      - (2). In wood, with or without addition of more or less rudimentary constructive nests: woodpeckers, nuthatches, and titmice (at times).
        - (a).[1] Partly constructive: petrels, sand martins, many titmice.
    - (b). Constructive, increment nests (mainly).
      - (1). The Statant, or "standing" type; supported mainly from below, and built from base, up. More primitive than 2.
        - (b).[1] Partly constructive. See 2, (b)[1] above.
        - (a).[1] Wholly constructive: typical of most Passeres, and of most members of other orders: robins, sparrows, most warblers, eagles, most humming birds, flamingoes, and gulls.
      - (2). The Pendent, or hanging type; suspended from side or from above; representing highest constructive effort in nest-building.
        - (a).[1] Wholly constructive.
          - (i). Pendent; adherent at side only by aid saliva or mud, as in eaves swallows and swifts.
          - (ii). Pensile: suspended from above only as in the rather stiff nests of vireos, or from above and at the side, as in kinglets.
          - (iii). Pendulous: elastic, and swinging free from one or more supporting points; orioles, weaver birds, and cassiques.
        - (b).[1] Partly adaptive, in reference to natural site: parula warbler, tailor bird.
          - (a).[2] Partly suspended, and often between upright supports; cup apparently molded on breast, as in fantail warbler; variable.
  - ii Associated or co-operative nests.
    - (a). Individual nests with common shield: in the sociable grosbeak of Africa aggregated to the number of 100-300 or more, of grass, in mushroom form. (?)
    - (b). Single nest-mass, representing a composite nest, built on the co-operative plan, by Ani, or black cuckoo of Central America; eggs deposited in tiers.

a true *nest*, though not necessarily of the most primitive type, even though their young never see their parents, and according to our view the nest-building instinct is wanting only in such birds as regularly make no preparations, or take no precautions to conceal or protect their eggs except through the aid of their own bodies or instincts. The ocellated Megapode (*Lipoa ocellata*), indeed, is known to prepare its nest with great care, and with a precision and uniformity hardly exceeded by builders of a higher order. A shallow depression is first scratched in the ground to a depth of eight or nine inches, with diameter twice as great, and the cup or saucer thus formed is filled with an overflowing mass of dead leaves and grass; upon this low pile the soil is finally heaped into a fairly even mound. Their large eggs, which are laid at rather long intervals, are regularly set in the same plane, and with their smaller ends turned down, around and within the "rim of the saucer," and but a few inches above the bed of fermentable leaves, first at opposite sides in form of a lozenge, and then in the interstices, until a circle of eight eggs is complete, all standing in the same plane, and with large ends up; at each laying this mound is successively opened at the top, and the hole as often filled in with sand.

By secondarily adaptive nests (*No. 2* of table 2), we mean any natural cavities used, with little or no change, for the concealment and protection of the eggs or young, and we regard them as the most primitive form of existing nests. In all such cases there are the instincts to conceal and otherwise protect, through choice of site, acts which lie at the foundation of all nest-building operations in birds; although such individuals may use no materials gathered from without, their chosen protective cavities, so far as instinct is concerned, must be regarded as adaptive nests. In many cases they are adopted without change (*No. 2*, a^1) but in other species they are quite as apt to be primarily adapted to the needs of the occupant by a greater or less amount of constructive effort (*No. 2*, b^1), and even by many species which under other circumstances excavate or put together the entire fabric themselves.

The third and highest class of nests, which naturally claim our chief interest (*No. 3* of table 2), are those which are primarily adaptive, or made to fit the needs of the builders, solely by their own efforts, through the aid only of such supports as nature

directly or indirectly provides. This great division is provisionally subdivided into (i) individual or independent nests, which with the possible exceptions to be later noticed, are due to the activity of a single pair of birds, and are occupied exclusively by the builders, and (ii) co-operative nests, which are to some extent built and used on a co-operative plan. Aside from certain of the mound builders, which have been placed in a separate section, and polygamous ostriches, in which a single cock with three or four hens usually unite in the production and care of the offspring, using a common nest, and sometimes producing as many as thirty eggs, the most striking illustrations are presented by the ani (*Crotophaga ani*) of the West Indies, and possibly by the sociable grosbeak (*Philhataerus socius*) of South Africa. Unfortunately exact and sufficiently detailed field observations are lacking in these remarkable birds, and no satisfactory analysis of their breeding habits can now be made. In the ani, several females with one or more (?) males occupy, (and presumably unite in building) a large nest which is placed high in trees. Each female contributes her quota of eggs, which are sometimes deposited in tiers and separated by leaves; the number of eggs, which depends upon the number of females actively interested, according to Scott, as quoted by Sharpe,[15] has been found to reach at least 21. If the habit of treating the eggs, as noted above is correctly reported, it suggests that such a nest may prove to be a composite, or series of superimposed nests, in reference to the activities of the builders. One bird having singly (or jointly) founded the nest and laid her eggs, is followed by another which satisfies her building impulses by adding leaves, laying upon them her own eggs, and so on. The observer, from whose account the preceding facts were drawn, further says: "In the first nest I examined, the eggs were in two distinct layers, separated by a deep bed of dry leaves; the bottom layer consisted of four eggs, and these strange to say, were all infertile." The last remark suggests that the eggs of a given tier are laid by the same bird.

The great mushroom like or umbrella shaped nests of the sociable grosbeaks or weaver birds have been often described; the aggregate has been found to contain as many as 327 individual nests, closely agglutinated and built around the branches

[15] Op. cit., p. 321.

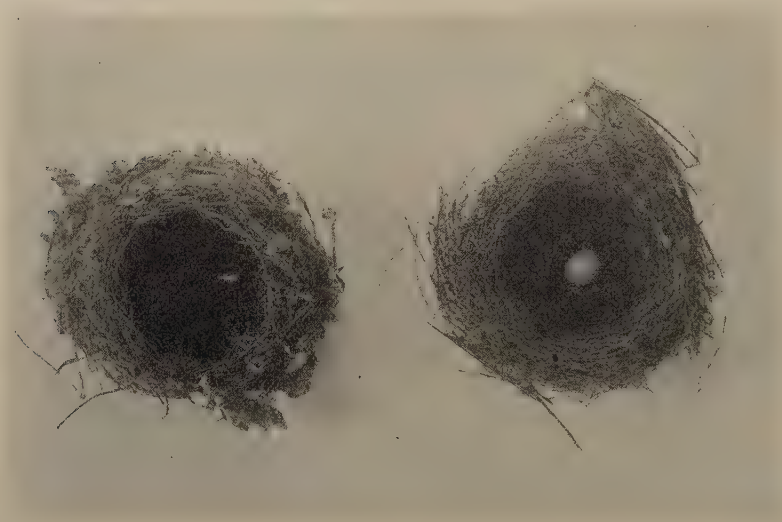
of trees which serve as support; the outer surface or "ex-umbrella," has the appearance of a thatched roof, suggesting the hut of a native, while the under side is perforated by entrance-holes corresponding to the number of nests in use. These aggregated nests are frequently used as refuge, and are occupied year after year, the mass growing by an extension of the "eaves," until they are thrown down or the tree gives way under the weight. It may prove that in this instance there is really no mutual aid rendered either in building a common foundation or in thatching a common roof, but that the nests though closely aggregated, are strictly individual units; upon this question observations at the present are conflicting.

We now come to consider the great division of individual, primarily adaptive nests, which are either mainly excavated, in earth (*i*, *a*, *1* of table *2*), the more primitive fashion, or in wood (*i*, *a*, *2*). The nest-chamber, however formed, is apt to be finished by a certain though variable amount of constructive effort, by the addition of a lining (*i*, a–a^1). In many cases, as in sand martins, the lining is reduced to an insignificant layer of feathers, dry grass, or rootlets, and suggests the relic, or echo of a time when other methods prevailed, and a nest was formed more completely upon the increment plan, though this interpretation, it is true, might seem to conflict with other facts.

It is to be further noted that birds which commonly excavate, such as many of the kingfishers, woodpeckers, and titmice, on occasion cut short or omit this work, and use a natural cavity with little or no change instead. Thus the American chickadee, which is often found in class *i*, *a*, *2*, not infrequently neglects the work of excavation entirely, and drops back to class *2*, b^1. Again bluebirds and hornbills adapt natural cavities to their needs, but in different ways, the former always constructing within them a more or less elaborate cup on the increment plan, while the former, as we have seen, merely reduces the opening, and smears it with a sticky secretion. Most of the woodpeckers which drill holes in wood in order to secure their insect prey, also drill other holes which they use as nests; accordingly it is not surprising to find that the rufous woodpecker of India (*Micropterus phaeoceps*) which riddles the mounds of termites for its food, will occasionally drill them to make a nest; nor is it strange that certain insect eating kingfishers

(*Tanysiptera*) of the East Indian and Australian forests have a similar habit, while the fish-eaters, when they do not casually adapt a natural cavity to conceal their eggs, tunnel the earthen banks of the streams off which they feed; in all such cases the methods of nest-building have to all appearances been influenced by the food habits.

The most elaborate nests of modern birds fall under what is preeminently the *constructive* type of building (*3*, *i*, *b*), and may be called *Increment Nests*, par excellence, because they are made of separate pieces or increments, brought and laid in



4 5

FIGURE 4—On left, nest of black-throated green warbler, *Dendroica virens*, removed from support; cup deep, perfectly molded, with overhanging brim; materials various, yellow birch bark covering outer wall; rather elaborate increment nest of statant type.

FIGURE 5—On right, nest and egg of magnolia warbler (see fig. 3), seen from above; loosely modelled of nearly uniform materials throughout, with horsehair lining; cup as perfect as in Fig. 4, but more shallow, and of different form.

succession, often hundreds or thousands in number, of indeed the most diverse kinds, though put together and treated in a fairly definite manner, and, as we say, with great ingenuity, deftness or art.

Considered in the broadest sense, the increment nests are of two kinds or types, based upon different methods of support

and correlated activities of the builders; namely: (*i*, *b*, *1*) the Statant [16] or *standing* type, which is supported from below, and built from its base or foundations, upward, and (*i*, *b*, *2*) the Pendent [17] or *hanging* type, suspended from above, or from the sides, and necessarily built downward or outward from its supporting points.

Increment nests (figs. 1–5) which are wholly, or partly the work of the builders, and which stand alone, whatever the nature of the site, are characteristic of the great passerine order,

FIGURE 6—Cluster of pendent usnea lichen on dead twig of pine, adapted for nest by parula warbler, *Compsothlypis americana*. (See table 2, —3, I, b, 2, b^1.)

as well as of most existing birds; in its simplest state it represents the most primitive form of nest, excepting only the simplest natural cavities, or those made only by scratching or stirring up the ground.

[16] The use of this heraldic term is not above criticism, but it will serve until a better is suggested.

[17] "Pendent" is used in the strictly literal sense of hanging, or suspended, but not as synonymous with *pendulous* or *penduline*, by which we mean swinging freely, and apply only to elastic suspended nests as of the oriole or weaver finches. "Pensile" is commonly used as the equivalent of "pendulous," though I have sometimes applied it to the stiffer pendent nests of vireos and kinglets.

Hanging or suspended nests when due wholly to the efforts of the builders, in what may possibly be regarded as their simplest form (*b*, *2*, a^1, *i*) are attached to their support by one side only, and often by the aid of viscous mud, saliva, or both. Under this head would fall many of the swifts, swallows, as well as certain hummingbirds which fix their diminutive nests to cliffs, drooping leaves, or even to swaying tendrils and cords, in which case the nest at times is even counterpoised by the addition of weights (see section 7). It is natural to find that here, as

FIGURE 7—Upper figure, nest of esculent swiftlet, *Collocalia nidiphaga*, soiled from use; composed entirely of saliva; pendent type, supported at side. (See table 2, —2, a^1, I.)

FIGURE 8—Lower figure, nest and eggs of American chimney swift, *Chaetura pelagica;* wholly of elm twigs, crossed and glued with saliva.

well as in nests of the subordinate division (*i–iii*, a^2), which are more or less transitional in character, that a molded cup form is present wherever the supports are sufficiently rigid to permit of the molding movements and render them effective.

More completely pendent nests (a^1, *ii*) are seen in the rather stiff cups of the vireos in which the brim is suspended between the slender forks of a twig. Although such cups are often very

regular, their symmetry is not the result of molding and turning movements, practiced with the stereotyped uniformity seen in all nests of the standing type. (See section 4.)

By compacting the soft cotton or down of seeds, or using similar products, the penduline tit (*Remiza*) produces a remarkable retort-shaped structure, which it suspends between upright twigs rather than from a forking branch; it has a tubular entrance built out from the upper end, while below is seen a pocket, thought by some to represent a "false entrance," and to be of use in warding off night attacks of lizards and snakes; according to such ideas, the sleeper when aroused by a "knock"

FIGURE 9—Pendent stiff nest of red-eyed vireo, *Vireo olivaceus,* showing suspension to forked twig, and character of cup and outer wall. (See table 2, —2, a[1] II.)

at the blind door, has a chance to make good her escape either by everting the tube or piercing the opposite wall.

The most highly differentiated forms of the suspended type of nest, with the possible exception of such admirable fabrics as the Remiza builds reaches the acme of construction in the truly pendulous, flexible "purse," "stocking," flask-, or retort-shaped cradles of the oriole, the cassique, and certain of the weaver birds. The wonderful nest of the Brazilian cassique (*Ostinops decumans*) in the shape of an elastic and greatly elongated guard, is swung to a bough by a single cord of woven grass, the whole sometimes reaching a length of six feet.

Swinging pendulous nests are seldom concealed, their position alone usually offering a sufficient guarantee of protection. In certain of the weavers of Madagascar and the East, hundreds of such nests are sometimes suspended from the same tree, which is often resorted to for years; again social weavers often hang their nests under the thatch of houses, and to find one nest suspended to another is not rare. The remarkable nest of the Indian weaver (*Ploceus baya*) is entered from below, and through a peculiar woven tube, which is carried several inches from beneath the body of the nest itself, and may even become compounded by the addition of successive chambers "infraimposed," or added from below. (See section 2.)

Increment nests of whatever type, may be canopied by some sort of a protecting shield, with entrance at the side or from below. In the singular nest of the South American oven bird, to mention an extreme case, the whole is a substantial chamber of mud, weighing eight or nine pounds, evenly smoothed and domed without, and with winding entrance passage opening at a point considerably below the cavity reserved for the eggs.

Do birds which commonly build from a basal support ever display a tendency to suspend their nest from the side or from above? As a rule they certainly do not, so far as recorded observations admit of any conclusions; in some cases they apparently do, as in tailor birds and certain species of the hummingbird family. There are cases in which the answer would appear to depend upon a definition of terms, with perhaps the splitting of hairs at that. Accordingly we shall find the tailor bird and the parula warbler, at times at least (i, b, 2, b^1) occupying pendent nests which are secondarily adaptive, or where the suspension is directly furnished by some natural objects such as lichens or leaves. The nest of this warbler (fig. 6) is certainly suspended, but it is simply made by slightly adapting a suspended body, in this instance by sewing together the free ends of a cluster of usnea lichen with rootlets. The tailor bird commonly draws together the edges of one or more leaves and stitches them in the form of a suspensory pocket, which is filled with cotton down and other soft substances and presumably molded after the common method; yet at other times it is said to make use of natural supports in the more usual way.

The fantail warbler (a^2) in a somewhat similar fashion binds together the free upright stems of grass in a way to form a support for a globular nest which is then built, with inner cup presumably modelled by the usual turning movements, finally bringing the grass together above its nest thus formed. This is certainly a very different form of suspension from that sought

FIGURE 10—Pendulous nest of Baltimore oriole, *Icterus galbula*, showing typical method of suspense, and treatment of outer wall.

by most orioles, weavers, and vireos, but it may represent a mile-post on the evolutionary road along which such forms as build more strictly pendulous nests have passed. Nests of certain wrens and of redwing blackbirds, which conform strictly to what we have called the standing type, are sometimes suspended between the culms of sedges or flags in a not wholly dissimilar fashion.

There are birds which build suspended or semi-pensile nests but without the effective weaving and compactness seen in either an oriole or a vireo. I refer to the kinglets. The golden-crowned kinglet (*Regulus satrapa*) fashions a rather large and loose nest upon and around a drooping cluster of twigs of some evergreen tree. One which I have particularly examined [18] is nearly spherical with entrance at top, and is composed of green moss (*Hypnum unciatum*), lichens from spruce bark, spiders' silk and feathers, and is lined with feathers and hair. When found it was said to be strong, light, and elastic, but seemed to lose its consistency upon drying. It was built upon a drooping spray of the black spruce, at a point about 1½ feet from the tip of the branch, 4 feet from the trunk, and 25 feet from the ground.

Magnolia warblers occasionally build what may be called pseudo-pendent nests; they are fixed rather weakly to forking twigs, and rest upon underlying sprays, which thus contribute to their support (fig. 3). Examination of their structure indicates that they are built from the base up, and not from the fork downward, and outward, as in a vireo. (Compare fig. 5.) They are rather thin and loosely modelled, but hold up their weight easily when the underlying twigs are cut away.[19]

It is not necessary to dwell upon the fact that a classification of nests does not usually accord with a classification of their builders; while in certain families the type form of the nest is fairly constant, in others it is highly variable, and this variation often extends to different species of the same genus. Of individual variation we shall speak in the next section.

[18] For this as well as for many other interesting nests I am indebted to Miss Cordelia J. Stanwood, of Ellsworth, Maine.

[19] For an account of the nests of this warbler, by Cordelia J. Stanwood, see *The Auk*, vol. xxvii, p. 384. Cambridge, 1910.

OBSERVATIONS ON TERMITES IN JAMAICA

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Division of labor amongst the free moving individuals of communities is not restricted to human society but is found in the social insects belonging to the two very different groups, Hymenoptera (ants, bees and wasps) and the Termites. In these there may be distinct castes with specializations of labor not directly connected with the reproductive functions.

Much has been done toward an understanding of the behavior of the Hymenoptera, but so little has been recorded regarding the activities of the Termites that the following notes may be of use, if but to call attention to the need of future exact experimentation in this interesting group.

At Montego Bay, Jamaica, B. W. I., the large, dark-colored nests of termites are conspicuous objects on trees and fences. Some 20 nests, each a separate community, were examined and the termites from them made the material for the following observations in July and August. M. Dr. Jules Desneux having very obligingly examined for me some specimens of the termites used in these experiments writes that they are probably the true *Termes ripperti* Ramber, belonging in the subgenus *Eutermes*.

Each community has three chief areas of activity, the nest, the passageways or "arcades" and the feeding grounds. In each community one finds individuals of the following castes; workers, soldiers, females, males, and also the young. We will briefly describe those three areas of activity and then the special functions of the different castes.

Taking first the important connecting link between the nest and the food, the dark-colored passageways seen on trees and stones radiating out from the nest for 50 feet or more, we may describe them as flattened arches forming side walls and ceiling over the termites as they pass to and from the nest. These passageways have the natural floor formed by the bark of the tree or surface of the stone, etc., but the sides and ceiling are constructed by the termites. The usual passageway, which we will call an "arcade" as being a covered walk not hollowed out as a tunnel but arched over, is about 7 or 8 mm. wide and half

as high, but from this size they run up to 50 mm. The largest may have several distinct passageways inside and seem to arise from union of smaller arcades which each contain but one cavity.

Through these arcades the termites run rapidly to and from the nest in small bands or flocks of less than a dozen which may, however, often fuse with those before and behind to make continuous lines. The termites do not stay on the right or the left but sometimes cross, thus creating unnecessary friction with files coming in the opposite direction. When the number running becomes great enough the individuals run two or more abreast and while usually on the floor the larger numbers may crowd the arcade till many run upon the ceiling as well and the arcade is full of the flowing multitudes always going in opposite directions, unless under some unusual stimulus of fright when they may pour along in one direction and soon leave the arcade empty.

The rate of locomotion was found to be about 15 mm. per second, or three lengths per second.

The way the termites construct the walls of the arcades was seen when old arcades were broken and restored, when new ones were made from nests transported to new trees and from experimental nests kept in aquaria or hung from the ceiling.

In constructing a new arcade there is first established a definite path along which the termites run for hours or days to and fro; then the sides of this path are gradually walled in, and finally a roof built over all. The first walls are laid down in sections of a few millimeters length at irregular intervals and irregularly right and left. These pieces are gradually connected and arched over: the part of the arcade nearest the supply of building material is completed first. Within ten days a much disturbed and decimated colony transported to a new tree built some nineteen feet of arcade. In normal communities a foot of destroyed arcade is replaced in a night. When the side walls are but 2 to 3 mm. high they are already arched inward over the track to form the beginning of the arched roof of the arcade.

The walls of the arcade are about $\frac{1}{8}$ of a mm. thick and externally covered with fragments from $\frac{1}{8}$ to 1 mm. in size stuck together by some dark material. Internally the walls are smoother and made more largely of the dark cement. Observing the termites we see that workers turn aside now and then to form the walls:

each deposits a mouthful of wood or other vegetable fibre of the above size and then quickly reversing skillfully ejects a droplet of dark liquid from the anus. This liquid rapidly loses lustre as if dried or coagulated and it fastens the building particles together as a dark cement. There is also some little manipulation with the mouth parts and palpation with the antennae. The tendency to use the two ends of the body alternately is quite strongly marked. No one worker tarries long at the wall but each may now and then make a slight addition of cement or of building particles or of both and then run rapidly along. The work is carried on as is the building of comb in the bee hive.

Under the microscope, it is seen that the building material is made up of vegetable tissue with its cells in their normal connection, that is not chewed or macerated apart, but merely in small mouthfuls.

In a transplanted colony the new arcades near the nest were made from the material of the nest together with skins of termites while the arcades at the food end, near the top of a cocoanut tree, were made of the fragments found amidst the bases of the leaves.

In many cases the termites were seen to pick up fragments of coral sand on the ground and run with them away from as well as toward the nest. Some of these were then used to add to the outside walls of the arcades, even six feet above the ground. Twenty-nine of these minute stones taken from an arcade newly built six feet from the ground, placed side by side formed a row 39 mm. long, the largest being 2½ and the smallest ½ mm. long. The largest weighed between three and four milligrams while a living worker weighed nearly five milligrams. No indication of any sort of aid was seen: each worker acting alone and just like any other. Each worked but a short time at any place.

While the arcade completely hides the termites from view it is not always light proof but when held up to the sky is seen to be filled with chinks where the cement does not fill in the spaces between the fragments. In old arcades these chinks seem to be filled up and the wall made more completely of cement as seen from the inside, and then but little light probably enters.

The arcades are subject to frequent destruction and need to be constantly repaired. Frequently they are abandoned and new ones constructed.

When the warping of an arcade throws it away from a branch a new floor may be constructed along the arch and then the termites run from the usual arcade out into a tubular bridge for some inches and then back to the arcade with its bark floor.

The floor of the arcade seems clean but when termites are confined in glass they smear it over with anal material before they can walk up it and escape. The suggestion of purpose and means in this case offers an interesting problem for future study.

The rate of arcade building was found to depend upon the readiness with which the termites could obtain not only vegetable tissue but also water. Without enough of these elements they would run for many days uncovered; and when only water was abundant there was more smearing of dark material over the path. Before any other sign there is observable a line of minute dark excreted drops along the sides of the trail to be followed by definite wall building. Hence we may suppose the building of the arcades is made up of the two factors, the need of discharging the effects of digestion, along the road, and the tendency to carry away some of the food material: the use of one end of the body being correlated with the use of the other.

When the arcades were punctured with a needle the method of repair was exclusively the application of the anal cement. In the minute hole there appeared first one or two antennae which seemed to measure the hole, then the anal end was presented and a drop secreted which tended to stretch across the hole but the surface tension film soon broke and the drop withdrew to one side and dried out as a crescent along the edge of the hole; then a second palpation with antennae, a second drop and so on until a fifth drop, or so, finally remained stretched across the the most minute remnant of the hole. It was notable that the successive drops were so placed as to close in the hole from all sides, after the manner of the portions of an iris diaphragm. Probably such cementing work finishes the smooth inside of the arcade which is comparable to a rough concrete wall faced inside with pure cement.

The second great area of activity of the termites is the region of food and water getting. The termites probably get water from dead moist wood and from dew and rain; in captivity they drink greedily from moist wood, filter paper, or stones and

soon die if deprived of moisture, so that the presence of water is a necessary condition in their life and probably one reason why the direct sunshine would not be favorable. The source of water supply was not found out in the case of some communities found living on mangroves far out in the salt water with but small areas of tree branches to depend on.

The food eaten is dead wood of many kinds of trees, including cocoloba, mango and mangrove, cocoanut, calabash, and especially logwood. The wood is not attacked at the nest where the bark of the tree is intact but at some considerable distance, where there is entrance into the interior from some accidental injury. The termites were not seen to enter through the bark, whose hard or varnished surface seems to repell their mandibles, but wherever there had been a broken branch or limb or a dead spot there the arcades might terminate in holes eaten into the wood. In captivity the above woods were eaten into mere shells about the tunnels and the same was true for imported pine wood and for sugar cane and the interior of bamboos, while but little attention was paid to bread or boiled egg, or dead fish or clams.

In eating the food only the workers were seen to be active and these remained a long time slowly chewing off a mouthful. In one case a marked worker (painted) remained in the wood twenty-one minutes before starting to the nest.

Having thus slowly obtained food and water the workers run through the long arcades to the third field of their activities, the nest or termitarium to which all the arcades lead and which is the home or breeding place and region of greatest protection and complete darkness.

The method of building the nest was not observed, but the outer surface of it is covered over with an unbroken layer identical with the arcade walls and the interior can easily be understood if imagined made up of many arcades built over one another in all directions with intercommunications and with thickened walls.

In the repair of nests as in arcade building nearby material is used. Thus when pine blocks, soaked in methylene blue, were thrust into the nest, the broken walls were mended about the block with use of some of the blue wood bitten off and carried a few inches.

Some of the nests are too large to be put into a barrel and too heavy to be lifted by a man. One, 1½ feet high and 2½ feet on the side of the rather quadrangular base, weighed 43 pounds, dry, without the contained termites and food store. When broken into, the nest appears like a sponge of dark material which is brittle but very tough and heavy enough to sink in water.

The newer parts of the nest are lighter colored and the older darker and more dense with less air space. In form the nest is globose or conical or more rarely spindle-shaped with the base, or one side, or the centre, applied to the tree trunk, branch or fence post, or the stone or ground, that is the substratum. The part near this substratum is the oldest and the most compact. While at first sight the passageways seem without any system they reveal more or less the plan of consecutive layers from the older part to the surface, at least in many nests and in some regions of the nest. But the presence of foreign objects, branches, leaves, etc., in the interior of the nest where it has been gradually built over these neighboring objects often makes the interior very irregular.

The labyrinths in the nest are often about 7 mm. in diameter with walls ⅓ mm. thick in all the newer parts of the nest; but the passageways are of very changeable diameter and shape and they communicate so frequently as to appear a mere sponge work. It is difficult to thrust in a straight needle more than 30 mm. without meeting a wall. In older parts of a nest we may break open chambers 30 by 40 mm. by only 7 mm. deep which may send out several branching passages 7 mm. wide on that same level. The walls here may be ½ to 1 mm. thick. The most completely lamellated parts of nests are made up of concentric stories about 7 mm. deep with walls that are ¼ to ½ mm. thick. In each story the passageways take on the character of curved, shallow chambers that may be 30 to 50 mm. on the level but only 7 mm. deep. The floor of one is the ceiling of another and such plates may be isolated as sheets of the dark papier maché matеterial of the above thickness and expanse. But such large approximately level pieces are quite exceptional, the usual fragment of the nest is always abruptly curved and of little extent.

In some most dense parts of nests the passageways may be reduced to 3 and 4 mm. in diameter while the walls are thickened

to an equal or greater measurement. When such parts are sawn open they present the appearance of old oak wood bored by insects and can be polished like wood of a fine grain.

This material burns like wood and leaves a white ash. It crumbles under the razor edge and under the microscope appears made up of fragments of vegetable cell-walls much comminuted and not in normal juxtaposition but impregnated with and surrounded by much amorphous dark material. In water much of the brown color dissolves out and more in potash, leaving the material soft. Macerated in potassium chlorate and nitric acid the nest material falls apart as pieces corresponding in size with the mouthfuls used in arcade building. Each piece is largely a mass of very small fragments of comminuted cell-walls. In the macerated nest material are many yellow setae from the termites. Some of the cell-wall fragments give the cellulose reaction with Schulz's Solution. By pulverizing, weighing and measuring the nest material it was estimated that in a certain nest the ratio of wall material to enclosed air space was about 1 to 2; and each termite would have more than nine times its volume of air and five times its volume of wall material as its individual share.

Some compound masses of arcades seen, built up one over the other, strengthen the supposition that the nest is of the same general nature as the arcade, but more elaborate in having the food material more comminuted and the anal secretion much more abundant.

Here again the factors underlying the building of the nest may be thought of as the bringing in of food and the need of disposing of excreta.

In every nest there was one chamber made with more care or of more definite form than any of the others and this was the place where the "queen" (laying female) was found, if at all. This special chamber is in the oldest part of the nest, at the base or on the side, and is well protected within the densest material, usually. It is easily recognized as having one nearly flat floor 30 to 40 up to 40 by 75 mm. wide and a distinctly arched roof 4 to 7 mm. above the floor. The ceiling may have a number of small rounded holes in it but the floor is all one expanse, but with lines upon it as if it had been reconstructed by the tearing away of former partitions and levelling of the

floors. Around the low periphery of this domed chamber are a dozen to twenty exits into neighboring chambers and passageways which may be from 5 by 15 or 20 to 3 by 6 mm. and with no system. The ceiling of the chamber seems thinner than the floor, perhaps; the ceiling $\frac{1}{4}$ to 1 mm.; the floor $\frac{1}{2}$ to 1 to $1\frac{1}{2}$ mm. The peripheral exits are rounded holes of small size, some are only 3 by 4 mm. In the neighborhood of these chambers, of which there is but one for each community, it is very evident that there is much reconstruction of the nest going on and this holds for other regions also. Thus there are incomplete partitions apparently in various stages of removal and minute windows from passage to passage only 1 to 2 mm. wide, which appear to be passageways that are being closed up.

One remarkable element in the nest was frequently found but not always, that is the stored up food masses described bv H. G. Hubbard in the Proc. Boston Soc. Nat. Hist., 1877, pages 267–274 and comparable to the "fungus gardens" of authors. These nodules are much lighter in color than the nest material and strike the attention at once as being concretion-like masses filling and replacing the chambers of the nest. At first they were thought to be fungus growths, from their color and evident slow concentric growth and filling up of the cavities. But microscopic examination reveals only such stray hyphae and fungus spores as might come on the surface from accidental contamination, while the central solid parts are purely such as might be made like the nest itself by the work of the termites. Reduced to fine powder or cut into sections the material of the nodules is seen to be bits of vegetable tissue mingled with a yellow amorphous substance. The vegetable tissue is in the form of fragments of cell walls, many of which give the cellulose reaction with chloriodide of zinc. The entire mass may be looked at as torn cell walls mingled with some material that may be secreted by the termites or else collected as food from some unknown source. It is a sort of vegetable concrete which falls apart in hot $KClO_2 + HNO_3$ into small masses of irregularly packed cell walls suggesting manipulated mouthfuls of wood in which all natural association of cells has been destroyed. These masses must be held together by some matrix or cement. Scattered through the macerated mass are setae from the termites.

The amount of this material is sometimes very great: one nest

contained nodules aggregating 3000 c. cm. as measured by its displacement of water. One nodule was about 10 x 10 x 10 cm. and weighed 450 grams.

These nodules are dense and like fine-grained wood and may be cut and polished like wood, with little grain, but yet showing a concentric lamination when broken.

They float in water but are otherwise much like the nest material, though of a very light color; they burn like wood, leaving a white ash. Examining different nests one arrives at the conception that the nodules begin as minute deposits of food material upon the walls of some passages in the older parts of the nest and then are added to little by little till rounded heaps begin to fill up the cavity of the nest there, then the mass is built out into neighboring passages, producing the round, branched nodules a few centimeters long and with branches 3–4 mm. thick which are often found forming loose-fitting casts of the passageways here and there. Later these seem to be built into nearly solid masses with botryoidal surfaces and this implies the removal of the walls of the passages filled by the nodule and the filling in of the space thus gained by the nodule material. A heavy round mass 70 mm. thick may result which, when sawed open, is nearly solid, with but few remnants of former walls and on the other hand this mass may lie nearly free in the nest, since the tearing down of walls may precede the growth of the nodule. In cutting open the nest such nodules readily fall out. Many, however, always remain joined to the walls of the passages and sometimes walls may be grown in and included in the outer parts of the nodule.

Some nodules come to have nearly smooth curved surfaces and no indication of being conglomerated from the contents of small passages. Such large globes, 100 mm. in diameter or more, are fastened to the walls of the nest only on one face and from this the termites gain entrance into the interior of the nodule when they use it as food. The termites eating out the inner parts of the nodule, leave a mere shell which suggests a woody fungus and is of brighter color on the inner concave face where roughened by the nibbling jaws of the termites.

Hubbard states that the young eat these nodules. In captivity the adults were seen to eat the nodules readily, and it was not determined how the young are fed.

In only one case was a fresh, white and not very hard nodule found and this was in a nest with several similar nodules 30 to 50 mm. thick but hard. The soft, white nodule looked much like some puff ball fungus when cut open and was 25 mm. thick. Sections of this show it to be a real fungus. It is possible that at times, as in the rainy season of spring, fungus may grow upon the above food nodules in amount sufficient to make them like real fungus gardens, but so far as seen this summer, they are primarily food stores and may be taken as representing the primitive basis of fungus gardens more highly developed in other climates.

That these masses of food store have nutritive value over and above the cellulose they contain is shown by nitrogen determinations kindly made for me in the Chemical Laboratory here. Various pieces of the food nodules yielded from two to three-tenths per cent of nitrogen, which would correspond to more than one per cent of proteid matter.

In connection with this occurrence of immense food surplus it might be mentioned that different communities present all stages of success and there are poorly kept and abandoned nests as well as some which are exceedingly well taken care of.

Frequently a large, yellow-red ant, probably *Camponotus hannani* Forel, takes possession of part of the nest even before the termites have abandoned it and introduces the added unpleasantness in study of the termites described by Hubbard.

Turning now to the inhabitants of the nest, we found many thousands of winged termites in some nests but most nests had none at all. These generally crawled rapidly into the dark and but few would fly; a few flew to the lamp at night, but these probably came from disturbed and transported nests. Hubbard records some Jamaica termites ready to swarm in February. The winged forms occupied some one portion of the nest, often toward the surface, and were densely crowded.

In the queen chamber of most nests one large deaelated female, or queen, could be found, though easily lost. In two cases four queens were found in one nest, apparently all in the same queen chamber. The queens in different nests varied much in amount of distention, the largest being 27 mm. long and 7 mm. thick. The abdomen showed slow but powerful vermicular waves of contraction and was so heavy as to be but slowly dragged by

the crawling movements of the legs. In captivity, in glass cells, the queens sought to get upon rough surfaces and to move away from light, following along in the stream of workers and escaping, if possible, even through small holes by long efforts.

The number of joints in antenna of the queen varied from 2 to 14 and was not always the same right and left. But even the winged forms in the nest may have 14 or 15 on one side and 9 or less on the other, so that the loss of joints is not necessarily connected with the assumption of sedentary life.

Each queen was surrounded by workers and soldiers and seen to be fed from the mouths of workers. The body of the queen gives off much moisture that condenses on the glass roof of artificial cells and must be replaced from the mouths of workers. That this exudation of moisture may carry with it substances that remain on the surface of the body of the female is suggested by the fact that some 20 or less workers constantly stand along each side of the queen and perform scraping movements with their mouth parts over the skin of the abdomen. A queen crawling along a road made by workers in an artificial nest was surrounded by more than 40 attendants.

The eggs are some quarter of a mm. or so in length and emerge from the female at the rate of about 1 a minute in clusters of 3 or 4 or more up to 7 or 8. They tend to collect in a mass at the point of issue but the workers were seen to seize the eggs in small groups and to carry them away. The eggs are very sticky and may adhere by chance to the heads of soldiers where they long remain, but normally they are taken in the mouths of the workers and much manipulated before they are carried out of the artificial cell to a distance of 1 or more inches and then they are fastened up against the ceiling. Over night 500 or 600 eggs were thus laid and carried away to be stuck in various clusters here and there.

While the soldiers were seen to work at the eggs as they issued none were carried off by the soldiers, except by accident as above stated.

In 2 nests were found deaelated forms that seemed to be males. One nest had 4 queens and 2 males and the other 4 queens and 1 male. However, other males may readily have escaped notice, especially as they were not particularly sought for. The nest with 1 male and 4 large, stout queens was a very populous nest

some 2 by 1 feet in diameter, conical. The male was near the females, probably in the queen chamber, and near this a dense cluster of some 200 large, dark-brown workers; possibly complemental forms? No winged forms were found in either of the nests containing males. The 2 males in the other nest were near the queens, which were small. The workers surrounded the males and tended them but not as assiduously as in the case of the female and in much less numbers. On a table a male moved with quick, restless action, but did not progress rapidly, twisting right and left, walking quickly hither and thither, soon going into the shadow of nearby objects. In the natural nest innumerable young in all stages were generally found not far from the region of the queen chamber. Occasionally small callows, 2 mm. long, were taken in the processions from transplanted nests. The distinct form of head of the soldier is early acquired in the white young.

The adult community is composed of workers and soldiers in about the ratio of 9 to 1. One nest 1½ feet high and 1½ feet wide contained 631,878 termites, as represented by the average of 3 estimates from weighing and measurements of volume of all the community. The great majority of these, probably half a million, were workers.

All the mechanical work of the community was seen to be done by this caste: the construction of nest and arcades, the tearing off and carrying of food, the transport of eggs, the cleaning of the queen and the male and also the feeding and cleaning of the soldiers, the feeding of the queen and finally the biting of all foes.

About every tenth termite is a soldier, a nasutus or form with black, prolonged head and minute jaws, having a gland that discharges at the tip of the snout-like termination of the head, as figured by Knower, J. H., Univ. Circulars, 1894. The use of this caste would seem to be connected with different development of sense organs rather than with muscular work. The nasuti might be called "investigators" for the community rather than soldiers, for though very effective in certain refined modes of defense their conspicuous function is to precede the workers in all new undertakings and also to stand between them and outlying unknown dangers.

Whenever the nest or the arcade or feeding ground is disturbed

nasuti become evident and by rapid journeys round about with outstretched antennae come into contact with the source of disturbance, if possible; the workers generally follow after the first rush of soldiers. When a new arcade is to be built the soldiers are seen stationed along the route in a row on each side, as many as 60 on the right and as many on the left of a stream of workers 225 mm. long. These guards stand at a large angle to the moving throng with heads out and palpating antennae. They are very easily affected by breath, or draught or touch. On disturbance the workers first retreat along the procession leaving only soldiers for a time. Also in the midst of a large mass of drinking workers a line of soldiers was found on each side of the stream of coming and going workers, so that the alignment of soldiers along moving processions of workers in an exposed place seems a deep-seated habit.

The soldier on guard may sometimes join the procession and some other ultimately come into his place, but the guards remain rather stationary for a long time.

In what way, if any, the soldiers influence the workers, was not found out. The rapid vibration of the body which makes the soldiers appear as blurs was not seen to produce any effect upon other termites, nor was any sound heard when this violent motion was going on. The workers also exhibit this vibration and in both cases it seems the result of some excitement, but was not seen to produce response in other termites. The soldiers being of lighter weight, exhibit this remarkable vibration more markedly than the workers and amidst aliens they seem to escape attack when appearing as mere blurs. One with right first and second legs and left second legs cut off still vibrated. The legs of soldiers were seen to be cleaned by workers and the soldiers raised the abdomen in a special attitude when a worker was cleaning the under side. Soldiers were seen to feed or drink from one another's mouths, but as they appear not to drink or feed from water or wood when kept several days isolated and then do solicit workers and obtain material from the workers' mouths it is probable that the workers are the necessary middlemen between the soldiers and the raw material.

Though the soldiers do not fight with their jaws they are potent defenders of the community, at least, against other communities. Nasuti were seen to attack alien nasuti and workers by thrusting

their snouts against or close to the enemy and ejecting a minute amount of liquid from the tips. This liquid is perfectly clear and colorless and dries on glass to leave a clear residue, as if some clear gum. Tested with congo, tumeric and litmus paper, red, blue and neutral, this secretion gave no color change. When a cover glass was held over excited soldiers this secretion was collected as if by squirting across space. When drops of it were projected by the soldier onto the heads of other soldiers and workers it seemed to produce a sort of paralysis, which in some cases was connected with the adhesion of the antennae to the head. Whenever the antennae of a termite were stuck to the head by water or were cut off the termite remained standing still without initiative and something of the same effect followed the attacks of soldiers. The secretion seemed to act merely mechanically to stick legs, etc., till the foe was powerless.

A very marked factor in the community life is the ability to establish and maintain trails between the food and the nest.

In the transplanted nests it was found that the workers and soldiers scattered widely at night as individuals and small bands as well as in larger streams and ultimately found food or means of escape, even along wires, etc.

When a nest was suspended for some days and no termites allowed to escape they poured out in great streams as soon as contact was allowed between the nest and the sand heaped up beneath it. Then radiating streams in all directions spread over the sand and established side anastomosing streams till a large network of moving processions explored all the available territory and found avenues for escape into distant parts of the building and the ground. From the first some termites returned along the line against the main current and some picked up and carried both centripetally and centrifugally, a few grains of sand. The soldiers almost always were in advance of workers in the radiating processions. Many tentative lines were abandoned and a few chief lines maintained. The very loose sand was packed down, or accidentally rolled aside, till a distinct groove marked the road followed by the termites.

From a nest transplanted to a cocoanut tree the termites spread out over the ground in the night and explored a wide area, but here as in the other case, in the day time the termites

either remained within the nest or ran only in the main roads that were laid down in the night.

The movements of a lost termite liberated in the middle of a wooded floor, where no termites had been, seemed quite random and not orientated by light or presence of table or walls. It ran rapidly and constantly in complex curves, often crossed its own trail without returning on it or appearing to be affected by it, sometimes running up the leg of the table and down again and later repeating this, sometimes in the shadow of the table and sometimes outside it; finally coming to a crack in the floor too wide to reach across, it ran rather steadily along this to the wall and under this.

When in company with other termites spreading out from the nest the termite finds the trail, or follows the track of the others, even when running alone and many inches from any others that have passed before. But an old track is not followed with the speed and directness of a new one constantly traversed.

The trail is followed not only on the solid bark or stone but on the loose shifting sand where the particles are very large as compared with the feet of the termites, being as small boulders to a man. But on smooth glass in an aquarium the termites do not progress readily; they cover the trail with excretions and in this way we saw them finally escape up the side of a jar as was discussed by Beaumont in Panama. In running along the trail the termites hold the antennae wide apart and downward, with oscillating movements. The palps also hang down close to the trail beneath the mouth.

Some suggestion of the nature of the means by which the termites follow the track of others may be got from the results of breaking the trail and the way the trail is found again. The following rude experiments were made.

A clean cover glass 18 mm. square was placed on a trail on horizontal boards when no termites were passing. Immediately the centrifugal or nest leaving workers came to the edge of the glass they bounded back and ran away toward the nest. The centripetal workers on the other side stopped and shoved against the glass. The soldiers stood by the edge of the glass and stretched out their antennae over its edge and also ran out laterally and investigated the neighborhood. No termites got upon the glass. Very soon one wandering soldier chanced to get to the accumu-

lating centripetal termites near the far side of the glass and then returned to the near side by a route some distance to the side of the glass . Then many termites ran the same side track and the procession was permanently established around the glass. Even when the glass was removed the procession continued to make the detour which for some days was a visible bend in an otherwise straight track.

At first the guards had stood in a row on opposite sides of the glass but when the procession moved in the detour the guards stood along each side of the procession and no attention was paid to the glass.

Thinking the termites might use some pine wood sawdust in making walls along a horizontal path on boards, some was dropped across the path. The workers at once stopped running and only soldiers were to be seen. These drew back and very cautiously felt toward the sawdust with the antennae; often one then turned tail and ran away. When a short train of workers came running up the trail they stopped as if shocked before touching the sawdust though they did not touch the soldiers nor were there any vibrating movements that might have given warning sounds. The workers seemed not aware of the danger till they almost touched it. Some soldiers from the first advanced around the sides of the sawdust and investigated with outstretched antennae and raised heads. Gradually some went nearly past the pile of sawdust. One worker finally picked up a fragment and carried it away, but the pile remained for days without further use while in a few hours the procession had reformed in a detour about the sawdust.

When termites were running rapidly on branching trails on the loose sand in spreading out from a tree containing a transplanted community the sand was disturbed by a stick drawn across the trail. The termites checked at the edges of the miniature gully as if against a solid object till, after several had accumulated from the sparse procession, a few ventured on in the same general direction as the trail and came to the old part of the trail, when the procession was resumed across the new sand. When the trail was depressed by the finger a similar gully resulted but the termites ran across this with much less delay as the material of the old trail had not been removed.

At a point, B, where a trail forked, 2 inches of the sand along

the trail were moved bodily to one side by a stick, leaving a bare space of fresh sand from B to A. The termites coming to the point of forking, B, continued along the other fork as if the fork, B–A, had never existed, but the termites coming back toward the nest when they got to A, accumulated there in the lack of any familiar trail over the two inches of sand to B. From A many returned on their footsteps an inch to a side path and slowly got off one side, 3 inches along this old side branch. Finally some termites partly rolling down the slope from A toward B and partly exploring in that general direction did arrive at the old fork beyond B. Here some ran toward the nest and some away from it along with the termites already passing. But almost at once after these had crossed the new sand there was a rapid rush of termites from A to B and soon some went from B to A, and the removed trail was reestablished in the same general line.

The effect of obstacles across the path was also tried by putting strips of manila paper and blades of grass across. A strip an inch wide and 11 long across a trail down a cocoanut tree caused all the termites to stop and recoil as if shocked; all above, that is toward nest, then ran back and left the trail entirely deserted. Those below were mostly soldiers and they accumulated in a cluster of 12 or so at the edge of the paper. Some wandered 3 or 4 inches right and left by the edge of the paper and some few got onto the paper and proceeded diagonally nearly across but when near enough to reach bark on the opposite side with antennae stopped as if shocked by change from paper to bark and returned. After 20 minutes none had gotten across. When paper was then removed the termites still stopped at line where paper had been till finally one soldier crossed and went slowly up tree along trail where no termites had been for 20 minutes.

A like strip but 5 mm. wide laid in the interval between gangs of termites running down the same tree the next day, 2 or 3 abreast, produced the same check in the procession both above and below. But here those coming up rebounded from the slightly raised edge of the paper and turned back till the track was deserted while those above collected to the number of 2 or 3 dozen. After 3 minutes 1 soldier crossed almost to the other edge; then a worker came up from below and crossed,

a second from above crossed and 2 more crossed, but yet the trail was not reestablished. The crowd that had accumulated above surged back 3 inches to an old side path and soon ran in it 5 or 6 abreast. Meantime some of them going along the upper edge of the paper got 5½ inches to the end of it and so around and back to the trail below, a soldier in the lead. At the end of 15 minutes there was a strong line descending around the paper and so by the old path to the ground, while but few crossed the paper and these checked as they came to the edge which was raised so the head of a termite might go in under it. But the next evening a slender stream of termites was going down the tree across this paper, and the edge was chewed somewhat. When running on a board the termites also bite off some of the roughness left on the sawed surface and so smooth their paths.

A pencil mark across the trail did not check the march but scraping off the surface of the board did.

A like strip of paper 4 mm. wide was put across a strong procession down the tree. After 1 minute of check a worker ventured across and a second and third followed, but several hundred crowded together at the upper edge and remained while many ran up and down across the narrow strip which is not the length of the smallest termite in the procession. But as soon as the paper is removed the crowd flows down like a liquid mass. When the same paper was moistened with saliva and crossed, above the former place, the termites hesitated much more and few crossed for many minutes.

The same paper pressed down across a trail on the sand caused scarce an instant's pause till the termites walked across. But at this same time, 9.45 p. m. scratching off the sand, even removing the white sand down to the dark earth, caused but little check and the termites soon crossed the new material, though on previous evenings at 8.30 they had been much more disturbed by such breaking of the trail. Apparently on the sand they may be more influenced by general sense of direction than on the tree and less by response to the trail and that at different periods of the daily rhythms of activity the relative intensity of these two factors may be different on the sand.

The daily rhythms have also a bearing upon the above recorded accumulations of termites above and below an obstacle.

These periodic changes from centripetal to centrifugal locomotion are in part described for these same termites by Andrews and Middleton, J. H. Univ. Circular No. 232, February, 1911.

Finally a like strip of paper but 3 mm. wide put across a main trunk line down the tree checked the whole procession for a whole minute before first one then another ventured across. Almost all were workers. One from above went ½ inch to left and then half across, 1 from below crossed on line of trail. Then traffic resumed in 7 minutes, but still many banked up on the upper side.

Even when running over the paper rapidly every one under the lens was seen to balk at the edge of the paper and to feel it with the palpi. Many also hesitated a bit on the paper before stepping off on the other side onto the trail. When the paper was removed some hesitated while many rushed across, some stood aside and examined the track but in 3 minutes most all rushed along without check. When this paper was put loosely across a continuous procession on the sand the termites passed along under it without check, and when the paper was pressed down in the sand there was but a slight check till all passed back and forth as if paper were not there.

Strips of grass across a track on tree acted like paper; strips cut 2 mm. wide caused little delay but those of 4 mm. long delay.

A smooth octagon pencil across track in sand caused the outgoing line to stop and act as if trying to get under it, or else to go along pencil to right or left. Some turned back toward the nest. On the other side of the pencil some turned to the left along the side of the pencil. After many minutes some from the nest got to the end of the pencil and made a wide detour of a foot in the direction towards which the old trail led; but they did not find the old trail. One worker climbed over the roughened metal end of the pencil, others followed and soon a trail was established over this part of the pencil. On removing the pencil a hesitating crossing from both sides lead to reestablishment of the old trail. Likewise a piece of smooth bamboo across the trail on the sand was not at first surmounted but the termites after many minutes went around it to make an accidental connection with another trail. Finally some did climb over and then the trail was resumed straight over the bamboo.

These observations might be interpreted as supporting the view that the termites run after the others along the trail from some chemical stimulus due to material left by the others and that the termites also have some sense of the direction in which they are running and an ability to continue on in that line even after detours.

A rather ludicrous result of the former factor, or at least, a peculiar exhibition of the running of termites one after the other was several times seen when many workers and soldiers were kept for days in a finger bowl with moist filterpaper on the bottom. They then sometimes after random running about, ran continuously for a half hour or more in a circle around the bottom of the bowl. Each followed behind those before and so on indefinitely in a circle about 9 inches in length, completing 1 lap every 15 seconds. Another lot, mostly soldiers, though kept several days in a dish with a large prickly pear "leaf" and thus familiar with the surroundings and lack of escape, took to running about the elliptical top surface of the leaf in an interrupted ellipse. Some stopped and stood aside while a few ran counter to the rest. After this closed circuit has been maintained some hours the leaf was hung up vertically in the sun to be photographed, but the running ceased, to be renewed, though in the opposite direction, when the leaf was restored to the dish. Finally most all went gradually down under the leaf though for some hours others kept on running irregularly and crossed various parts of the leaf.

Though much of the activity of the termite is influenced by stimuli from the immediate neighborhood, by chemical substances apparently, which may produce something akin to a sense of smell, or at all events cause the termite to act as if it had a sense of smell, there are disturbances starting far from the termite and affecting it while affecting us as sound and light.

In a community suspended from the ceiling by a copper wire and represented by many thousands on a moist block of artificial stone which they got to from the nest by means of a long stick as a bridge it was first observed by Mr. Middleton that the noise of thunder and of blasting rocks was followed by a quick and very remarkable departure of most all the termites toward the nest. The blocks of stone weighed some 16 pounds

each and rested in a large zinc pan of water on a firm wall of stone and cement from the ground, so that it seemed likely that the concussion of the air came to the termites directly and not as a tremor of the stones they were clustered on. The same precipitate flight of the multitude of termites from these stones to the nest along the bridge was brought about by dropping a board upon the concrete floor with a loud crash. Even the clapping of hands which probably shook the stone foundation but imperceptibly served to drive the termites back to the nest. At first many termites ran into rather complex arcades built over the food rather than direct to the nest. The entire multitude could thus be driven completely into the nest in a few minutes. Attempts to influence the termites by blowing horns of various pitches near them failed though considerable disturbance of the air was produced.

That the concussions which affected them might be received by special organs is shown by the existence of a special organ in each of the six legs of the worker and the soldier; an organ comparable to the so called ear of the grasshopper.

Again, though the workers and soldiers have no eyes they respond to light by keeping away from it as a rule. When a hundred or so were kept in a finger bowl with moist filterpaper on the bottom and sides the termites collected after long migrations over the entire paper, in a cluster on the side toward the light where they were shielded from the light by the thickness of the paper. When kept in a long rectangular glass some 6x 4 x 12 inches in diameter, they always came to rest in a cluster on the bottom of the glass along the edge furthest away from the light (there being moist filter paper only upon the bottom of the dish). If then the dish was covered half by glass of one color and half by glass of another color the termites came to rest under one color or the other or in two clusters, one under each color. When the colors used were blue and green, or blue and yellow, or green and yellow, or green and red or yellow and red no constant preference was seen; but when the colors were blue and red the termites collected under the red only. It thus seems probable that termites respond differently to wave lengths of different length. The winged forms in the nest have eyes and as far as noticed always sought to run into holes or into the shadow of some object. But in a dark storm, some at 4

p. m. became more active and flew out of a bowl. A few came to lamp at night.

The responses of termites of one community to termites of another are most remarkable, as long since described by Beaumont in his observations in Panama. When one or more termites are removed from a community and returned after hours or days of isolation they are received back into the community without marked disturbance of any kind, generally seem not to be noticed at all. But a termite from another colony is generally at once set upon and killed.

The fighting response to alien termites was observed, by taking termites from one natural nest and placing them on another, by putting termites from one part of a community, kept in a finger bowl, into another like artificial colony from another nest, and finally by putting single termites with single termites of another nest. In all cases the result was death to the alien termites or to the others, or both, with the following exceptions:

One nest was found in which all the individuals seemed to lack the fighting reaction towards members of some other nests, though they would attack members of certain other communities.

In some nests individuals were found apparently lacking in the tendency to fight aliens, but these individuals were few. Such lack of response to aliens was also artificially brought about by washing termites in water, as described below. Very young termites of alien communities were examined carefully but not attacked; the young being immune to attack up to certain amount of development or at least of size. White larvae, $1\frac{1}{3}$ mm. long, greatly excite all alien workers which chance to touch them with antennae, but though pushed and licked they are not bitten. Yet a larvae 2 mm. long was surrounded and had leg bitten off while biting back into faces of aliens.

In spite of these exceptions it seems that one of the most certain actions of these termites is to attack termites of alien communities. These fighting responses were called out between various members of the communities. Thus workers attack: alien workers, soldiers, winged forms, males and queens as well as winged forms recently deaelated. Soldiers were seen to attack; soldiers, workers, winged forms; but the only experiment with an alien queen resulted in the abrupt retreat of the soldiers

after coming close to or in contact with the queen. Winged forms attacked workers and soldiers. Two queens in the same community rested in contact with one another without apparent response but an alien queen seems to have been bitten by a queen. In all cases the attack is apt to be accompanied by defense, but both attack and defense varied much in intensity.

As above mentioned these fighting responses to aliens were observed partly in the field and partly in laboratory conditions. In the field termites were carried from one nest to another and put on the outside after breaking a hole in the covering layer of the nest. The soldiers that rushed out of the nest ran quickly, in rapidly changing courses, over the surface of the nest but seemed to pay little attention to the aliens which also ran wildly about, but when the workers emerged from the nest they attacked the alien soldiers and workers, killing some and dragging others into the nest. Soldiers, however, were seen to point their heads at alien workers and soldiers and this probably meant the discharge of secretion upon the aliens. When many termites, winged forms as well as workers and soldiers of this broken nest were carried to a third nest and dropped onto it after breaking the outside surface the same attack was made by these inhabitants. The winged forms, however, were little noticed and rapidly entered into the interior of the alien nest or ran into some shaded retreat and came to rest.

Two communities, hung up by wires side by side and kept within the nest for some days, carried on a wholesale attack and defense, or war, when a stick was placed to connect the two nests. The termites from the larger nest swarmed along the stick to the smaller nest and met the outcoming aliens in vast numbers. For several days the termites continued to fight on the stick, with many killed dropping off, and then the larger community withdrew to its own nest and the smaller community did not go out far on the bridge.

When a colony of some thousands of one community was kept in a finger bowl and then allowed to pass by a paper bridge into another like bowl inhabited by a colony from an alien community the invaders fought the aliens at the point of contact. Here many did not stop to fight but passed on to explore the new bowl but ultimately the number of contests increased over a larger area. By the next day all the surviving termites

seemed to be of the invading colony, which was the stronger numerically as well as in aggressiveness.

The generally used method of observing the fighting response was to take a single worker or soldier from such a bowl colony, A, and put it into another bowl colony, B, afterwards one from B was put into A. In all the usual cases the 8 possible forms of the interaction were found: these may be stated as follows, w indicating a worker, s, a soldier and X an observed fight: wA X wB, wB X wA, wA X sB, sB X wA, sA X sB, sA X wB, sB X sA, wB X sA. The intensity of these contests was various and in some cases more or fewer of the combinations were lacking from failure of some individuals or whole colonies to be aggressive or even to resist attack.

In a few cases the fighting response was so strong that it was well exhibited when a single termite was placed with a single alien in a small arena, made with moist black paper on the bottom of a solid watch glass. In these cases of very strong inter-communal action one worker would at once attack the other and be as vigorously replied to so that when the two met or were pushed into contact they at once rose up with jaws clenching jaws like two fighting carnivores.

In one case a worker thus killed two others of a strongly hostile community in quick succession, by single combat with each as introduced. Generally no fighting response was called out between single termites in strange environment, and the bowl method, where one colony was at home, gave more certain results. On the other hand, a termite may be apparently lacking in response. Thus a very hostile alien amidst passive termites was seen to cut a hole into shoulder of abdomen of a mild worker which stood quiet during the operation.

In the fighting two acts are prominent: biting with the mandibles, squirting with the head gland; the former is confined to the worker and the latter to the soldier.

When an alien is placed amidst termites it may fall upon the first it comes into contact with or it may run some distance amongst the termites before attacking; on the other hand it may be seized by the first termite that meets it or it may pass some or many before it is seized, or attacked. A large worker may kill three others before it is itself killed.

The actual acts of the worker in attack or defense are to

touch the alien with antennae and then instantly, or after a longer interval, to seize it with the mandibles either violently or mildly. The mandibles often engage the mouth parts of a foe and the two stand with locked jaws till after some time one may have its mandible bitten off or be injured by loss of blood. Again a frequent point of attack is along side where one of the legs is seized by the knee and bitten till it separates, then a second leg may be cut off at the knee. A third place of attack is the anterior or the posterior part of the abdomen and a long continued biting there results in the loss of blood and death with shriveling of the body. An introduced alien commonly becomes the centre of interest of several or many termites which surround and examine it and 5 or 6 may at once seize it. In this way an introduced worker was lifted out with several alien workers clinging to it, biting its legs or cutting into its abdomen, and not removed without tearing the introduced worker to pieces.

When an alien runs about it may be followed and overtaken by attacking termites, and if lifted out the attacking termites seem to search for it for a short time.

The method of attack and defense shown by the soldier was to point the head at the foe, touching it or nearly touching it with the tip of its snout-like gland nozzle and then to eject minute drops of clear liquid onto the head of the foe. The drops were sometimes seen at the tip of the snout and then on the head of the foe, but more often the secretion first became visible as very minute droplets on the head of the foe. Over the head of the foe these droplets sometimes lay in lines as if squirted some distance through the air. This secretion seemed to daze the foe or to inconvenience its movements; sometimes this was visibly connected with the sticking of the antennae to the head. In this way the antennae might become so adherent that they would break rather than come loose when the loop was pulled with a needle. The drops adhered to vegetable fibre and could be pulled out as a viscid substance.

Returning to the consideration of the interactions of entire communities as indicated in the bowl experiments, we first noticed exception to the general hostility of termites to aliens in the case of two communities taken from trees a quarter of a mile apart, which we will call communities 1 and 2. Members

of these did not fight much with one another and the termites in 2 were especially mild, refusing to attack members of 1 at all, while members of 1 would mildly attack members of 2. The workers in 1 were small and light colored, those in 2 large and dark colored; possibly the differences are of specific value or more than differences of age.

But members of these 2 communities tested with members of 7 other communities gave various results, which all showed that 1 was more vigorous and 2 less vigorous in attack and defense; but certain colonies were obnoxous to both colonies and certain other colonies not attacked by either.

Representing by the small numeral the introduced termite and by the large numeral the bowl of aliens we found the following interactions of 1 with 2—9, and of 2 to 1—9 communities.

$_{1}2$=notice.	$_{2}1$=slight attack.
$_{3}2$=notice.	$_{3}1$=attack.
$_{4}2$=surrounded.	$_{4}1$=mild attack.
$_{5}2$=notice and cleaning of a worker by alien worker.	$_{5}1$=attack.
	$_{6}1$=violent attack.
$_{6}2$=violent attack.	
$_{7}2$=slight attack.	$_{7}1$=attack.
$_{8}2$=slight attack.	$_{8}1$=slight attack.
$_{9}2$=notice.	$_{9}1$=notice.

That is, the termites 1 showed more hostility than did 2; some colonies, 4 and 9, were but little attacked by either 1 or 2; one colony, 6, was violently attacked by both 1 and 2.

When 9, which was only noticed and not attacked by 1 and 2, was put with 6 there was a violent fight, in fact one worker of 9 killed two successive workers of 6 when pitted against them isolated in a small arena. 6 was especially aggressive to some others: thus individuals of 8, but slightly attacked by 1 and 2, were seized by the throat in 6; again 6 attacked 9 though 1 and 2 did not.

It thus appears that different communities have different grades of hostility, variously directed towards other communities.

Would not a complete knowledge of the interactions of a group of communities enable one to trace their probable phylogenetic connections?

The responses to aliens are not the same to all members of any community and this is markedly true of the two castes, workers and soldiers, since in a great many cases the soldiers are attacked when the workers are not or but slightly. The soldiers seem thus to bring out the fighting reaction more strongly than do the workers, as a rule.

The phenomena of artificial mixed colonies must also be taken into consideration. When a worker from a colony, 12, was put into another, 13, and vice versa, there resulted fighting, but when several thousand of 12 were thrown into a bowl with about as many of 13 there was little fighting and a mixture resulted in which no fighting nor dead were seen in the follow-night and day.

Yet the members of this mixture were of two sorts as shown by their reactions to the parent colonies. Some tested separately had retained the character of 12, that is, they were attacked when put into 13 but were not attacked when restored to 12. Others were attacked in 12 but not in 13, and might be said to have belonged to 13. The termites of community 12, which had two queens, were smaller and more aggressive than the larger, milder termites of 13, which had one large queen. In the mixture one could often recognize the two sorts by their sizes, but not always. Both soldiers and workers, though living without fighting apparently, with the alien community, were attacked when put singly amidst the pure aliens that had not been associated with the other colony.

When a large mass of the pure element, 12 or 13, was put into the mixture there was some fighting at the periphery of the introduced clump, but this was temporary. When a single worker or soldier from the pure colony 12 or 13 was put into the mixture it was generally noticed but rarely attacked. However, a dead queen from 12 put into the mixed colony was attacked by some and cleaned by others; put then into 13, was surrounded and bitten by three workers which held to it when removed; returned to 12, was surrounded and preened but not bitten.

The termites of this mixed colony had not lost response to a third community; a worker of a community, 10, put into 12 was attacked, transferred to 13 was mildly attacked, and then put into the mixture was attacked; a soldier of 10 was attacked

in 12, mildly attacked in 13 and slowly attacked in the mixture. While the associating of 2 communities together may thus lead to a state of armistice, some experiments to infect one colony by proximity to the other, so that its reaction factor would be changed, failed. That is, when 5 termites of 12 were kept 17 hours in close proximity to hundreds of 13 by caging them in a small hole in sugar cane covered with bolting cloth, in a bowl inhabited by 13, the separate workers and soldiers taken from the cane cage and tested all reacted amicably to 12 and hostile to 13, apparently just as if they had not been near the aliens. In some cases a termite returned to its fellows after fighting with aliens was attacked mildly by its fellows. This may have been due to infection amidst the aliens or to response to the wounds the termite may have received. After 4 days the above mixed colony was reduced chiefly to the component 12 by death of many 13, but this was not due to renewed fighting since there was a corresponding large mortality of 13 in the pure colony.

Then some young, 2 mm. long, from the mixture and some soldiers with white heads were also attacked in 13; being too old to expect immunity.

Bearing also upon these responses to aliens as opposed to members of a community are the responses to dead termites and to fragments and to mutilated individuals. As above noted the dead queen may evoke the same sort of responses as the live queen, for a time at least, but sometimes the response to the dead and wounded may be combined with the reactions exhibited in arcade building. When a mass of crushed termites was placed amidst aliens they responded by snapping the mandibles and in some cases the workers also turned about and deposited excreta upon it. In this case the use of mandibles and of excreta suggested that seen in the building of arcades, and the response was different from that to living aliens.

Mutilated aliens and pieces of them usually escape attack if they do not move. Thus when the antennae of a winged termite were cut off the termite was rarely attacked amidst aliens unless it had so far recovered as to walk or was made to move by being shoved with the forceps. (The loss of the antennae produces a state of inaction only slowly recovered from.) In the same way a soldier with its antennae cut off to the third joint and

walking but little was not attacked. When, however, a winged form happened to come against a worker and then bit the worker it was seized by several workers though it had attacked and was attacked without its antennae.

When the palps were cut off, the winged form was attacked. When the legs were cut off the winged form was attacked only when it wriggled but not when still. When the abdomen and metathorax of the winged form was cut off it was examined but not bitten till moved with the forceps. When the abdomen of a soldier was cut off it stood up and was attacked while also squirting clear liquid at the alien workers. When the head and wings were cut off it evoked snapping responses and excitement but no real attack; and when the head was cut off from the soldier it stood up but did not move and was not attacked though causing excitement.

The several organs were not attacked unless made to move by the forceps; this applies to the wings, antennae, legs, head and abdomen of winged forms and of soldiers.

It would thus appear that in the ordinary response to active aliens the two elements of movement and of alien character may be more or less combined and also that in case of severe injury to an alien either something inhibits the response to the alien character or else this character is itself affected along with the bodily injury. When the termites are incited to attack a moving torso or other fragment they soon desist and act more to it as to a moving brush or forceps than to a moving alien. A soldier that seemed as if asleep when put amidst aliens was attacked but soon left alone when inert, was again attacked when shoved against a worker but again soon left alone; here again the action of the alien seems a potent factor in the result.

That some chemical substances bring out responses in termites seems to follow from the effects of treating termites with ether: they readily fall into a trance and when recovered are received, both workers and soldiers, by members of their community as if not treated, but if they are returned to the community while under the ether they form the center of a group of termites that examine them with the antennae or even lick them a little. Likewise some juice of the stem of a mango on a worker caused its fellow workers to draw back and then stand pointing their antennae at it.

That most enthusiastic observer of termites, Beaumont, carried on experiments in Panama that led him to state that the termites he studied had a special odor for each nest and that even a piece of nest material from an alien community was responded to differently from a piece of the own nest. Later the interpretations of Bethe and others have strongly upheld the view that the ants respond to aliens through reaction to some nest stuff or aura peculiar to each community. All the foregoing observations, many of which but confirm the observations of Beaumont and upon the same or similar species, may readily be taken to support this view as applied to termites. At the same time it seems rash to affirm that there are not other factors than chemical substances affecting the termites to lead them to reply to aliens as they ordinarily do. Vibrations of various kinds and movements of air may also be potent. Future discoveries as to sounds produced might lead one to assume a special shibboleth for each community.

One of the most remarkable discoveries of Beaumont was that a termite washed a few minutes in water and returned, after drying, to its fellows was attacked and injured by a fellow termite; then a second worker cut off its head and turning about deposited anal material upon it; but he says there was no such general disturbance as there was when aliens were put on a nest.

Such results were many times obtained with the Jamaica termites and there is no doubt that water may greatly modify the responses of termites to one another, but the phenomena are complex and by no means readily analyzed without much more carefully guarded experiments with measured elements.

Considering the differences in amount of the response of various communities and the differences between its expression in various individuals it is not to be expected that the same results will always follow the same treatment of all termites. There were many failures to obtain any result by washing the termites, but in general thorough washing had the result to change the behavior of the washed termite as well as to change the responses it evoked both from its fellows and from aliens.

The well-washed termite is markedly below normal; it walks less actively and is not aggressive. The responses it calls out from its fellows are: unusual notice, examination, and even more or less attack which may end in severe injury and some-

times be accompanied by acts like those in arcade building, namely, ejection of material from the mouth, reversal of the ends of the body and ejection of anal material upon the wounded comrade. On the other hand such a washed termite placed amidst aliens is not attacked as an unwashed one is but is but mildly attacked. In general the well washed individual is injured both at home and abroad.

A rather typical experiment was as follows. Six or 7 termites in a fold of bolting cloth were washed 4 minutes under a $\frac{1}{4}$ inch tap of rapidly running water, 30 pounds pressure, and then drained off 4 minutes on filter paper. One worker put then amidst its fellows was mildly attacked, had a leg cut off, was bitten and had light-colored mouth material put upon its head. It did not defend itself and appeared as if sleepy. Transferred to an alien colony it was again attacked and had red-brown excreta put upon its head and throat by an alien worker which turned again to put more upon its abdomen but deposited a droplet on the filter paper. Returned, near dead, to its fellows, it was again mildly nibbled. More energetic attacks followed if the alien was amidst many washed termites. Thus a fellow worker placed amidst 18 workers and 2 soldiers washed as above, ran rapidly about and attacked the first washed one it touched, but gradually ceased to attack and tried to escape. And when an alien worker was placed in the same group it cut off the 2 antennae of one washed worker and cut the abdomen of another. Restored to its own community it acted nervously but was not noticed.

This effect of washing to make a termite somewhat offensive to both friends and foes was found to last in termites dried 80 minutes, but there are no experiments to show how soon it might have worn off.

Failures to get the above results from washing were observed when termites were washed 3 times as above and again when 20 and 200 were washed at once, and when a few were left two hours in a tumbler of water.

On the other hand, when the termites were soaked 15 minutes, $\frac{1}{2}$ hour, or 1 hour, in freshly gathered rain water the result was different in degree. In many of these soaked termites a neutral state seemed attained. These termites were carefully examined by fellows and by aliens but in some cases not attacked, so

that the water seemed to have made the termites somewhat different to their fellows but not obnoxious, while it made them acceptable to aliens. Here again there was the interesting gradation that the workers were more completely neutral while the soldiers called out more attack response and were more roughly treated by aliens and also by fellows, being jostled or pushed or snapped at but not bitten.

Assuming a nest aura we may suppose the water removes some substances and thereby so modifies this aura that the termite lacks the material to excite the aliens and also lacks the material to make it unnoticed by its fellows. It may thus attain to a state of near non-existence amidst aliens and of more or less unrecognized novelty amidst its fellows, according to the completeness of the loss. Mere wetness may, however, act to suppress, or to keep in, the aura. It is also to be borne in mind that the changed activity of the washed termite will cause it to bring forth less response than the more active normal one, while in as far as it is abnormal in any way it may evoke responses associated with shutting out the external, as in arcade building. The washing may also have caused physiological changes with new secretions, masking the normal ones or calling out new responses. Changed vibrations might also enter into the problem as well as the mere loss or change of some chemical substance, or nest aura.

The addition of a little ether, gasoline, or scented soap made no observed constant difference, but the termite thus washed was either only observed or else mildly attacked by its fellows and sometimes accepted by aliens with mere examination.

Assuming the reactions to other termites to be due to substances that come off in the water it might be possible to restore these substances or to apply them to termites so as to alter their normal aura and change the responses.

Many attempts to deceive the termites in this way were made, but with unsatisfactory results. When the juices from crushed termites were applied to an alien washed in water the responses to it by its fellows and by aliens were apparently the same as if it had only been washed in water, but there may have been undetected differences since the responses to dead or wounded and to washed termites seem to be much alike, so that the effect of the alien juices would be overlooked.

On various occasions many termites were put into small volumes of water and either shaken or allowed to stand till a yellowish or whitish opalescent liquid that might smell strongly of termites was obtained. When alien termites were put for a few minutes in this liquid they generally evoked the same response as when soaked in pure water, but there were some cases in which the solutions seemed to have specific effects. In these cases the termite moistened with the wash from aliens seemed to be more violently attacked by its fellows than if it had been only washed in water. Moreover the length of immersion in the liquid need be but brief compared to the time necessary to produce results by washing, as a rule. Such termites were also notably immune to attack amongst their fellows in whose liquids they had been immersed, while this was not often the case with washed termites. However, few very decisive results came out of these experiments, since it was difficult to distinguish between the results of washing and of immersion in foreign extracts.

In some striking cases workers wet in alien extract were surrounded but not attacked amidst the aliens, while a dry worker thus treated was violently attacked. Even when the wet worker attacked the aliens it was immune to their attacks, so that it suggested a wolf in sheep's clothing attacking the sheep but not attacked by them. Of course, here again, the mere wetting may have affected the aspect of the termite so that it called out no response from the aliens, though it plainly was affected by them. That is, the aliens may have neglected to attack the termite wet in juices from their own fellows, not because they were deceived by a familiar aura, but because they were not stimulated by the foreign aura which had been in some way annulled by the wetting.

Evidently there is need of experimentation to solve the many questions that arise in connection with these termites.

SUMMARY

1. A community of *Eutermes ripperti* is made up of workers and soldiers chiefly, may be half a million in number, and as these castes have no immediate concern with reproduction, are without eyes, and lack the specialized structure of the higher groups of communal insects, it would seem that study of their

activities might contribute to better understanding of factors underlying communal life.

2. These termites spend their energy chiefly in eating wood, at a distance from the home nest, and in running at about the rate of 15 mm. per second from nest to food and back, concealed in arcades.

3. The arcades are built by them from bits of wood cemented with anal discharges.

4. Each worker does as any other without any aid, as far as seen, and does but little at one time or place.

5. The nest may be thought of as aggregates of arcades, connected to form a spongework of chambers some 7 mm. wide and rarely 30 mm. long without abrupt turns and intercom-munications.

6. The material in both cases is primarily wood and secreted cement, but differs in the amount of comminution.

7. In each nest there is one specialized chamber some 7 mm. high and 30 or 40 mm. wide in which the queens or laying female or females are found.

8. The respiratory needs of the termites would seem slight, since the estimated amount of air in a nest weighing 40 pounds and occupying nearly 4 cubic feet of space was only 9 volumes for each volume of termite.

9. The "fungus gardens" often present in the nests appeared at this summer season as dry masses, used directly as stored-up food and not as substrata for fungus growths. They are, microscopically, finely comminuted fragments of cell walls of plants bound together with some secretion. They may, in this state, represent the primitive form from which culture gardens have arisen under other climatic conditions.

10. The nest is occupied by: many young and eggs; generally 1 but sometimes as many as 4 perfect females; 1 or 2 males (as far as seen); often many winged forms; and some hundreds of thousands of workers; and one-ninth as many soldiers, which are nasuti.

11. The workers do all the mechanical work: bite off and transport the wood; feed the soldiers, and males and females; clean the males, females and soldiers; remove the eggs from the orifice on the end of the female and clean and transport them; do all the work of arcade and nest building and all the biting in defense of the community.

12. The soldiers do no mechanical work, except to move themselves; they appear first when the nest or arcade is disturbed, they explore what is novel, lead the advance of processions, stand placed like guards along the sides of processions. They respond to anything unusual rather by exploratory advances than by retreat; being the quicker moving and more responsive members of the community. They form the "investigator" rather than the soldier caste. Yet they fight, in a refined way, by ejection of a secretion that binds the enemy fast.

13. Termites wander about in the night and find new food-supplies outside the protecting arcade. Processions are formed which may ultimately be covered over by arcades. In running after one another the termites keep the trail as if guided by chemical substances left by the others which passed before. But they also show an ability to continue on in the right direction even after detours when the trail has been destroyed.

14. There is evidence that these termites are affected by concussions of the air, leading them to retreat to the nest after thunder, etc.

16. They showed response to light by collecting where the light was least. Under colored glass of greatly different wave lengths they collected under the shortest, that is, "preferred" red to blue.

17. The interesting observations of Beaumont on the reactions of termites to alien termites are here verified to a large extent.

18. The young, up to certain development, are immune to attack, but the adults are attacked by all adults of any other community (but perfect males and females were not actually seen to attack, though they are attacked).

19. Individuals as well as communities differ in degrees of aggressiveness and this is not equally called out by all other individuals or communities.

20. Soldiers generally call out fighting response more intensely than workers do.

21. In extreme cases two workers isolated from two communities may be pitted like fighting cocks, each responding to contact with the other by use of the mandibles that leads to quick death of one or the other or of both combatants.

22. Soldiers respond to aliens by ejecting clear and apparently harmless liquid from the frontal gland, but it adheres to the alien and binds him fast.

23. When large numbers were mingled with large numbers of aliens at once, the normal fighting response was not seen.

24. The discriminations seen, between response to fellow members and to aliens, admit of interpretation on the hypothesis of a nest aura, or emission of substances characteristic of all but the youngest members of each community; at the same time movements of air, character of motion and vibrations emitted by aliens may yet be found to play important part in this discrimination.

25. Termites washed in water act unlike normal termites and call out responses from aliens and fellows often different from the normal.

26. Often a well-washed termite is attacked both by aliens and by fellows.

27. While we may ascribe the results of washing to removal or masking of a nest aura, other factors may be important.

28. Termites may respond both to injured and to washed termites by a use of both ends of the body like that in the building of arcades and this suggests an internal association of their actions toward many things agreeing chiefly in being external to or different from the nest aura.

29. Attempts to restore to termites hypothetical substances washed off led to confusing results showing the need of more exact experimentation.

30. This preliminary reconnaissance of the activities of these termites favors the view that chemical environment may be peculiarly potent for these creatures.

The enormous waste inseparable from such a non-nitrogenous food as wood provides the opportunity for utilization of the surplus and wastes in architecture.

Not only, according to Grassi and others, may the diverse castes be developed from like embryos by differences in food given them, but the whole adult community may be held together and marked off from what is foreign by response to substances which enable the termites to distinguish their own and to use the wood material in emphasizing the line of demarcation.

Nevertheless it is to be expected that examination will reveal that besides the chemical environment influences of vibrations and mechanical contacts are potent through the whole life of the community.